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Owl responses to habitat change at the landscape and regional scale and effects of weather in east central Alberta

by

Stephanie Robyn Grossman

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Environmental Biology and Ecology

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Date: Aug 25/03

ABSTRACT

The purpose of this study is to determine the large-scale responses of owl species to changes in habitat availability and configuration. I studied the relative effects of forest configuration and amount of forest on owl presence and abundance at the landscape scale (3X5km) in east central Alberta. I also examined the effects of regions (120X105km) on owl populations. Weather conditions that might affect owl detections were also examined. Responses of Great Horned Owls, Northern Saw-whet Owls, and Barred Owls to differences in forest configuration and amount were variable across regions, and the effects of regional differences were very strong. Habitat amount was more important than any combination of configuration variables for all three species, though in some cases the support for this conclusion was not very strong. Threshold responses to forest amount were only apparent for the Great Horned Owl, which increased in abundance from 0% to 60% forest cover, beyond this threshold their abundance dropped. Weather and timing variables affected detection of both Great Horned Owls and Northern Saw-whet Owls. Great Horned Owls were more likely to be detected at warmer temperatures, lower wind speeds, and later in the evening. Northern Saw-whet Owls were more likely to be detected in high forest cover, low temperatures, earlier in the season, and when both temperature and forest cover were high. In conclusion, owl abundance was more responsive to forest amount than configuration and it was clear that regional habitat characteristics were important for owls and need further study.

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CHAPTER 1

Thesis introduction

INTRODUCTION

Habitat availability and fragmentation

For the last 20 years ecologists have been examining the impacts of habitat fragmentation on avian populations. Habitat fragmentation occurs when portions of suitable habitat become increasingly interspersed with patches of non-suitable habitat (Wilcove *et al.* 1986). This phenomenon is composed of two elements: changes in the spatial distribution of habitat patches across a landscape (configuration) and a decrease in the total amount of habitat. Any impacts of habitat fragmentation on populations can occur because of the distribution of habitat as well as its availability.

The potential implications of habitat fragmentation on bird populations are many. Possible consequences of highly fragmented landscapes include an increase in forest/non-forest edge, which may be less desirable for nesting and may facilitate the intrusion of nest predators and parasites. Also, small patches of forest may contain no interior habitat, thereby excluding some species from nesting (Whitcomb *et al.* 1991). On the other hand, the potential implications of habitat loss are relatively straightforward: less habitat equals fewer birds. Understanding the relative magnitude of each process has important conservation value. For example, if the configuration of habitat is more consequential for bird populations than habitat amount then we may be able to alter the spatial distribution of habitat to mitigate the impacts of loss of habitat.

The relative importance of habitat configuration versus habitat loss on bird populations is hotly debated. Many researchers, especially in eastern North America,

claim that habitat fragmentation is the leading cause of avian population declines in North America (see Whitcomb *et al.* 1981). However, other researchers, mainly in western North America, are not finding severe fragmentation effects on bird populations (Schmiegelow *et al.* 1997).

Threshold responses to habitat loss

Andren (1994) changed the focus of this debate drastically when he published a meta-analysis of studies on the impacts of habitat fragmentation on avian and small mammal populations. His analysis suggested that the regional habitat context in a study area had significant influences on the responses of birds and small mammals to changes in habitat fragmentation at the landscape scale. When regional habitat is relatively high, bird populations respond mainly to habitat availability, and not at all to habitat fragmentation at the landscape scale. However, once regional habitat availability falls below a critical level (he suggests 30% to 10% of the landscape), then populations begin to respond more strongly to the configuration of habitat. As well, the type of land-use in the region may also affect the response of avian populations to changes in habitat availability and configuration (Mönkkönen and Reunanen 1999).

In essence, Andren proposed that populations may exhibit a threshold response to habitat loss instead of the previously supposed linear relationship. Habitat thresholds occur when small changes in the amount of habitat produce a dramatic ecological response (Turner and Gardner 1991). Andren's analysis suggests that populations may exhibit a linear relationship to habitat availability up to some threshold. At this point abundance will decline rapidly when populations begin to respond both to habitat availability and habitat configuration. Andren suggests that this threshold represents the

point at which species begin to respond not only to changes in habitat availability but also to changes in habitat configuration.

Theoretical models of threshold responses to habitat availability

In a review of modelling efforts to predict the effect of habitat configuration effects on extinction thresholds, Fahrig (2002) found various outcomes. Some models (e.g. With and King 1999, Hill and Caswell 1999) predicted huge impacts of fragmentation on the extinction threshold, while other models (that often included population dynamics, see Fahrig 1997, Flather and Bevers 2002) predicted much smaller effects of fragmentation. For example, With and Crist (1995) found that species' life-history was important in determining the location of the response threshold (measured by the point when populations switch from a random to an aggregated distribution) to habitat loss. Habitat specialists became aggregated when habitat amount was ~45%, while habitat generalists remained randomly dispersed until habitat fell to ~20%. They found that dispersal ability also influenced the threshold where populations became aggregated, suggesting that responses to habitat configuration may be based on species specific life history traits. In a second modelling exercise, Fahrig (1997) found that the amount of suitable habitat had a greater impact on extinction probability than did configuration, and that fragmentation effects were only expected when the amount of habitat fell below 10% - 30%.

Empirical evidence for habitat thresholds and the relative importance of habitat loss

Empirical tests of the presence of threshold responses in birds have been few and the results are variable (see Schmiegelow and Mönkkönen 2002 for a review). In general, there appears to be support for both the relative importance of habitat loss versus configuration and the presence of a response threshold to habitat loss (Trzcinski *et al.*

1999). However, studies continue to show the importance of habitat configuration on bird populations (Villard *et al.* 1999, Donovan and Flather 2002).

Owls and habitat configuration and loss

The lion's share of this work on the relative effects of habitat availability and configuration and population threshold responses has been conducted on passerines. Information on the response of other bird species to regional habitat changes is lacking, and especially so for owls, with the possible exception of the Northern Spotted Owl (*Strix occidentalis*). Both Hunter *et al.* (1995) and Lehmkuhl and Raphael (1993) found that Spotted Owls were strongly associated with contiguous forests and avoided forests that were highly discontinuous or fragmented. However, more recent work on the response of spotted owls to habitat characteristics by Meyer *et al.* (1998) showed that fragmentation effects were secondary to the overwhelming importance of total habitat availability on a landscape level. The Tawny Owl (*Strix aluco*) may be able to mitigate the effects of forest fragmentation by increasing home range sizes, thereby making them less sensitive to habitat configuration (Redpath 1995).

Owls have significant potential as flagship conservation species; they are easy to census and are often used in habitat assessments (Noss 1999). Some owl species may also be sensitive to changes in habitat availability and configuration (e.g. Barred Owls, *Strix varia*) given their year-round residency and specialization for mature interior forests (Mazur and James 2000). Also, sensitivity to thresholds may be, in part, determined by a species' habitat specialization and dispersal. While Barred Owls may be habitat specialists, making them more sensitive to possible thresholds, they are also extremely mobile, which may provide a buffer against possible fragmentation effects. It is,

therefore, important to understand the possible implications of threshold responses to habitat change in owls if we are to be able to use them as an indicator of habitat quality.

Great Horned Owl

Great Horned Owls *(Bubo Virginianus)* are the most common owl in North America, with a range extending throughout the continent. They are considered to be habitat generalists, using both forested (nesting, roosting) and non-forested habitats (hunting). Similarly, they are generalist consumers, and will eat a wide variety of prey species from voles to ducks, though they are known to prefer Snowshoe Hare (*Lepus americanus*) where their ranges overlap. Other preferred prey items include voles, mice, and ground squirrels (Rohner *et al.* 2001)

Northern Saw-whet Owl

Northern Saw-whet Owls *(Aegolius acadicus)* are also a common North American owl, with a range extending from eastern Canada and along a narrow band of boreal/sub-boreal forested habitat from Ontario to British Columbia. Habitat preferences for this species are poorly described, but they are known to nest in areas of mixedwood and deciduous forests. They are cavity nesters, often using abandoned woodpecker or flicker nests. Great Horned Owls are known predators of this small owl, and nest predation by corvids may occur. Prey species are restricted to small rodents such as mice and voles (Cannings 1993).

Barred Owl

Barred Owls *(Strix varia)* have a more restricted range than either the Great Horned or the Saw-whet Owl. Though their range extends throughout eastern North America, they inhabit only a narrow band of forested habitat in prairie Canada, but are more widespread in forested mountain areas of western Alberta and British Columbia.

These birds are known to be strongly associated with old mixedwood forests, and may have specific habitat requirements for mature forests with large snags or live trees for nesting. Preferred prey species for this owl include mainly mice, voles and squirrels, with some small birds and amphibians (Mazur and James 2000)

Thesis organization

The lack of data on the response of owl species to landscape and regional habitat changes represents a significant gap in landscape and avian ecology. In Chapter 2 I present an empirical analysis of the response of a community of owl species to both the amount of forest and its configuration at the landscape scale. As well, I will examine the potential for a threshold response to habitat changes and the possible implications of the regional forest context on species responses. The results of this study will be important in evaluating our understanding of owl populations and our ability to use this suite of species as an indicator of ecological condition. In Chapter 3 I examine the potential impacts of weather conditions on owl detectability, and in Chapter 4 I provide conclusions and management recommendations from this work.

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CHAPTER 2

Population responses of owls to changes in forest cover and configuration in east central Alberta

INTRODUCTION

Habitat fragmentation

The effects of habitat fragmentation on wildlife have been the focus of much ecological work over the past 20 years. However, results have been variable; some studies show fragmentation has a strongly negative impact on population size or community composition and others find no effect (see Schmiegelow and Mönkkönen 2002, Harrison and Bruna 1999 and Paton 1994 for reviews). Habitat fragmentation is composed of two elements: changes in the configuration of habitat (i.e., its spatial distribution across a landscape) and a decrease in habitat amount (Forman 1995). The potential implications of habitat fragmentation on bird populations are many, including an increase in forest/non-forest edge (Saunders *et al.* 2002), which may facilitate the intrusion of nest predators and parasites (Murcia 1995, Saunders *et al.* 1991), and the creation of small patches of forest (Saunders *et al.* 2002), excluding some interior forest specialists from nesting. The potential implications of habitat loss are relatively straightforward: less habitat equals fewer birds. The relative magnitude of each process has important conservation value. For example, if habitat configuration is more consequential for bird populations than habitat amount then the spatial distribution of habitat could be used to mitigate the impacts of loss of habitat. Hence, determining the implications of habitat fragmentation on population persistence requires an understanding of the effects of both habitat configuration and loss.

Andren's (1994) meta-analysis of fragmentation studies suggested that population responses to habitat fragmentation is determined by the total amount of habitat and that a threshold response in population size exists somewhere between 30% and 10% habitat availability. Population size responds linearly to the amount of habitat in the landscape until at the threshold habitat availability falls below some critical amount and population size decreases rapidly. Above this threshold there were no (or very weak) fragmentation effects, and below this threshold fragmentation effects become stronger, and the population size will decline rapidly (Andren 1994). Similarly, theoretical modelling efforts based on percolation theory suggest that thresholds may exist at ~59% habitat availability (Gardner *et al.* 1987), with this value fluctuating based on species-specific habitat interactions (i.e., dispersal, habitat specificity) (With and Crist 1995).

Empirical models of threshold responses to habitat availability

Empirical evidence supporting results from these modelling efforts are few and results are varied (see Schmiegelow and Monkkonen 2002 for a review). Trzcinski *et al.* (1999) found that for songbirds, forest amount consistently explained more variation and had a larger regression coefficient than forest configuration for all but one species, based on data collected from the Breeding Bird Survey (BBS). Few species showed an increasing response to forest configuration as forest amount declined. Donovan and Flather (2002) also used Breeding Bird Survey data to test the relative importance of forest cover and configuration and found conflicting results to that above. They found that throughout the eastern U.S., bird species that had a larger proportion of their breeding population in highly fragmented regions showed more dramatic population declines over time than species who bred mainly in unfragmented landscapes.

Owls within the framework of threshold responses to habitat

The great majority of the work on thresholds has focussed on passerines (Schmiegelow and Monkkonen 2002). Owls are a poorly understood taxa, yet they may have potential as an indicator of habitat condition given their longevity and large spatial habitat requirements (Newton 1979). As well, they are relatively easy to census compared to many songbirds (Hannon and McCallum unpub., O'Connell *et al.* 2000). This longevity and slow turnover rate of individuals may enable land managers to interpret population changes as being directly related to environmental change over time (Landres *et al.* 1988). The delineating of threshold responses may provide information on critical habitat amounts required to sustain populations of species, and may help determine the effectiveness of manipulating the spatial configuration for population sustainability.

In Alberta, most owl species are resident, have very large home ranges, and are quite mobile. Population fluctuations of residents can be tied directly to changes in a single habitat, whereas changes in populations of neotropical migrants can be influenced by changes in both breeding and wintering habitat (Lambeck 1999, Noss 1999, Landres *et al.* 1988). Resident species with large home ranges are often also considered to be of important conservation value due to their ability to function as umbrella species for other taxa that use similar habitat (Lambeck 1997, Noss 1999, Caro and O'Doherty 1999, Fleishman *et al.* 2000). Also, many owl species may be quite sensitive to habitat amount and its configuration. For instance, Great-horned Owls (*Bubo virginianus*) and Northern Saw-whet Owls (*Aegolius acadicus*) regularly forage along forest edges (Rohner and Krebs 1996, Cannings 1993, Bosakowski *et al.* 1989) and hence, may be sensitive to the amount of forest edge in a landscape, whereas Barred Owls (*Strix varia*) may be more

affected by the amount of forest habitat available for nesting and foraging (Takats 1998). Owls, then, are important taxa to study given their potential sensitivity to habitat change, indicating changes in habitat condition, and their function as umbrella species, with home ranges covering that of many other species (McLaren *et al.* 1998). However, because of the mobility of owls and their close ties to prey populations, teasing out habitat relationships may be difficult

While some of the finer scale habitat associations of owls are known there is very little understanding of the landscape or regional habitat associations of this group of birds. Here I define landscape level as being approximately 15 km^2, and regional as over 12,600 km^2. This study addresses some of the landscape and regional issues arising from the work published by Andren (1994) for the community of owls in east-central Alberta. Specifically I address the following questions:

1. Does regional land cover affect the response of owl populations to habitat availability and configuration?
2. Does the presence and/or abundance of owls respond primarily to habitat availability or habitat configuration at the landscape scale?
3. Is the presence and/or abundance of owl species responsive to specific habitat configuration metrics?
4. Is a threshold response to habitat availability evident in owl populations? If so, where is this threshold on the habitat availability gradient?

I expect that the regional land cover context will affect the response of owl populations to habitat availability and configuration. I also expect that these responses to habitat availability and configuration will be species specific, though habitat availability will be generally more important than habitat configuration. Threshold responses are expected in

the range of 10% to 40% forest cover. As well, I expect that regional forest cover will impact the response of species to landscape level habitat changes, such that decreasing regional forest cover will increase the importance of configuration and cause thresholds to appear with decreasing forest cover.

RESEARCH METHODS

Study area

This study was conducted in 3 regions across east-central Alberta: Ministik, MSTK (53°38'N 112°50W); Meanook, MNK (54°33'N 113°20'W); and Lac la Biche LLB (54°24'N 112°6'W) (Fig. 2-1). The regional context was defined by the largest study area (Lac la Biche: 12,600 km^2) and then applied around all study areas. All three of these regions were located within the transition zone between Aspen (*Populus tremuloides*) parkland forests to the south and boreal forests to the north and consist mainly of deciduous Aspen forests. Within each region there was a variable amount of agricultural and other human land-uses, see Table 2-1 for an outline of the percent land use in each study area. Data were collected at some study areas in each of 3 years (see Table 2-2 for an outline of the sampling across years and study areas).

Ministik

Ministik is located approximately 45 km east of Edmonton, Alberta and includes Elk Island National Park and the surrounding region. The park represents the largest area of forest in the region containing three major ecotypes: boreal mixedwood forest, aspen parkland, and riparian/wetland areas (Parks Canada 1999). The entire region (~12,600 km^2) was composed of approximately 25% forest cover, while the majority of the remaining area was used for cattle grazing and hay production with some

Table 2-1. . Landcover types of 3 regions in east central Alberta. Values presented here are percentages of each region (12,600 km^2) taken from the Landsat imagery described below. Classification accuracy at this level of detail may be lower than that for the rest of the analysis, but is provided here as an approximate comparison of the three regions landuse.

Region	Forest	Pasture	Crop	Wetland	Shrub/Grass	Clearcut	Burn	Water	Urban
Lac la Biche	55	5	7	28	1	1	1	2	0
Meanook	45	11	20	5	1	1	8	4.5	4.5
Ministik	25	25	35	2	7.5	0	0	3	2.5

Meanook

Meanook (due north of Ministik and west of Lac la Biche) is also at the northern edge of the aspen parkland/mixedwood boreal forest transition zone. Like the Lac la Biche region, aspen and mixedwood forest with considerable wetland/riparian areas were the dominant forest types at Meanook. Regionally it has approximately 45% forest cover, with the main anthropogenic land use being agricultural (largely cattle grazing with some wheat production).

Description of the spatial data

Classified Landsat Thematic Mapper 5 images of all three study regions were created from Landsat TM data from 1997 – 1999. Bands 1 through 5, and 7 (Stephen Hamilton, pers. comm.) were used to discriminate land cover in all areas, all bands have a resolution of 30 m. Band 6 was excluded due to its lower resolution (120m), providing no extra information for the classification (Brook and Kenkel 2002, Jensen 1996).

The data were classified using an unsupervised hierarchical classification technique with a minimum 25m resolution for the Alberta Ground Cover Classification (AGCC) and a 3X3 majority filter was applied. This filter is applied to increase accuracy of the dataset, though some very small habitat elements may be lost (McClain and Porter 2000, Saura 2000, Stallings *et al.* 1999). The Ministik dataset was further refined for accuracy with the cross-tabbing of over 500 field data points. The accuracy assessment for all datasets was approximately 85% for the dataset as a whole, though accuracy rates vary to some degree across cover classes (Arturo Sanchez-Azofeifa pers. comm.). The classification of all databases was then collapsed into 2 categories: forest and non-forest. Forest included all deciduous, coniferous and mixedwood forests, as well as treed bogs. Non-forest included water, roads, shrub and grass, urban, agriculture, pasture, un-forested

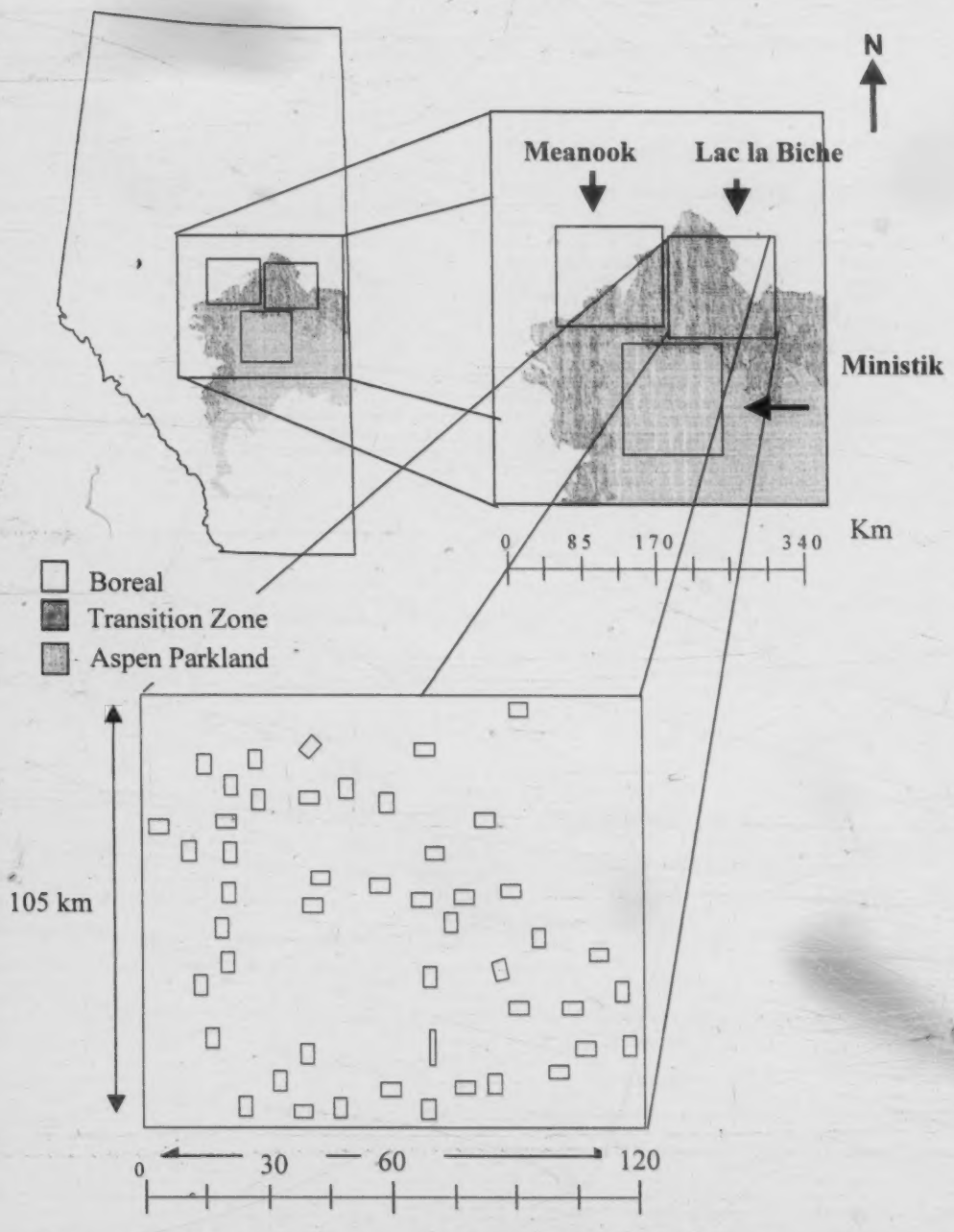


Figure 2-1. Study regions along the aspen parkland/boreal forest transition zone in Alberta. Each region is approximately 120km * 105km. The smaller rectangles are 3X5 km landscapes (see Fig. 2-2.).

and undifferentiated wetland, recent burns, and clear-cuts.

Experimental design

Within each of the 3 study regions 45 to 50 landscapes, each approximately 3 by 5 km were chosen to represent a gradient in forest cover. The 15 km^2 landscapes were chosen to fit, as closely as possible, to the distribution outlined in Table 2-3. I sampled more landscapes within the 10% to 40% range of forest cover because this was where I expected to find the most variation in species presence/abundance, and where threshold responses were predicted based on Andren's (1994) analysis. Landscapes were spaced at least 2 km apart to avoid sampling the same individuals in 2 different plots. Two km is the distance of the diameter of the expected territory size of Barred Owls (~3.5km^2) (Olsen 1999) in the area. To ensure that all forest patches represented comparable habitat I also attempted to control for the degree of disturbance within forest patches. Landscapes with high ungulate disturbance in the under-story were excluded from the possible set of landscapes.

Within each forest cover category (Table 2-3) I attempted to encompass a range of forest configuration variables. The possible range of configuration values within forest cover categories will be greatest in the moderate range of habitat availability (e.g. 30% to 60%), with minimal variation possible at either extreme level of habitat availability.

Winter nocturnal owl surveys

Owls were monitored using a playback technique, where recordings of con-specific owl calls were used to elicit responses from territorial birds. Before beginning owl surveys I calibrated the volume of the CD player to control for the difference in the transmission of sound in landscapes with varying degrees of forest cover. To ensure that

the same area was being surveyed in all landscapes I first determined the maximum distance an observer could hear the playbacks in highly forested landscapes at the maximum volume of my CD player. This volume, projecting a maximum of 700m, was then reduced in both medium and low-forested landscapes to maintain this same maximum distance.

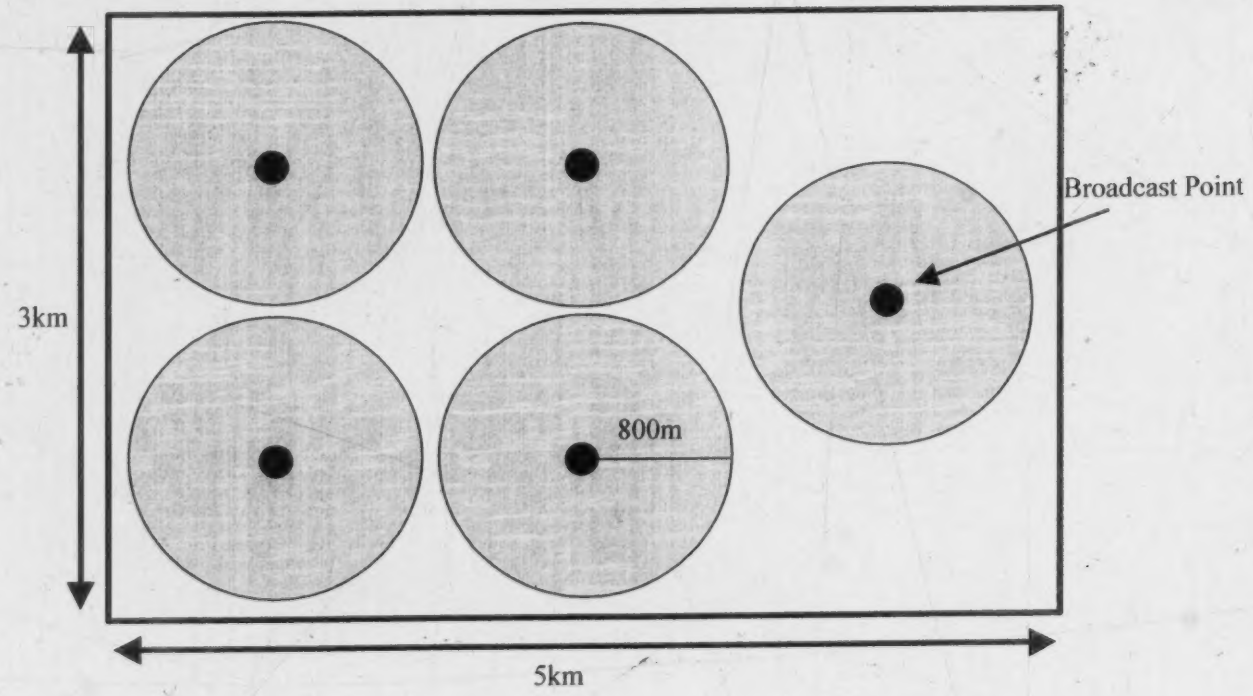
Five broadcast points were set up in each landscape to survey owls (Fig. 2-2). The broadcast stations were separated by 1.6 km, a distance slightly greater than the maximum distance an owl call could be detected (Bondrup-Nielsen 1978). Surveys were conducted from late February through to the end of April with two rounds conducted at each plot. In Alberta Great Horned Owls are the earliest nesters, beginning in late February (Johnsgard 1988). All other Alberta owls in this study are most actively breeding between March and April and are most vocal during this period. As well, to control for possible temporal variation in owl responses I interspersed the plots of different forest covers over time in each round.

One to two observers conducted owl surveys beginning 30 minutes after sunset and continuing for a maximum of 8 hours, playing a CD recording of vocalizations of expected owl species (Table 2-4). During the first round at each station I played call tapes with each call being broadcast once in each of three directions (N, ESE, and WSW) to elicit responses from nearby owls. In the second round the order of the points was reversed. The playback tapes were designed with 20 – 30 second recordings of owl calls

Table 2-3. Distribution of landscapes along the gradient of forest cover. This design is intended to concentrate sampling between 20% and 60% forest cover, where I expect to see the most dramatic change in owl abundance.

Forest Cover (%)	Number of Landscapes
80	4
60	4
55	4
50	4
45	4
40	4
35	4
30	4
25	4
20	4
15	4
10	4
Total	**48**

Figure 2-2. Landscape design with five broadcast points.



interspersed with 1-minute periods of silence. Long-eared Owls *(Asio otus)* and Great Grey Owls *(Strix nebulosa)* were not included on the tapes until the second round because they breed later than other species in central Alberta (Olsen 1999). The Great-horned Owl was excluded from the tapes due to its propensity to respond to the call of hetero-specifics (Bosakowski and Smith 1998) and the possibility it could reduce the response rate of other owl species it preys upon. After recording the estimated distance and direction of owl responses, I then scanned the area with a high-powered flashlight to locate birds that came in to the playbacks but did not vocalize. During each broadcast session environmental variables affecting owl behaviour were recorded, i.e. wind (Beaufort Scale), cloud cover, temperature, precipitation and moon visibility. Owl surveys were not conducted in high winds (≥3 on the Beaufort scale), or if there was considerable rain or snow.

Data analysis

Determining affects of weather

In Chapter 3 I found that Northern Saw-whet Owls did respond positively to an interaction between temperature and forest cover. To examine if this interaction would confound the analysis in this chapter I ran a Spearman Rank Correlation between temperature and forest cover. The correlation was performed separately for the data in Round 1 and Round 2. This analysis was performed in SPSS version 11.

Configuration metrics

Forest cover and configuration values were calculated using ArcView 3.2 and ArcMap 8.0 and Fragstats (McGarigal *et al.* 2002) at both the class (land cover type) and landscape level, with some modifications noted below. Forest patches are identified, in

Table 2-4. Play list for owl surveys CDs for Round 1 (Feb-March) and Round 2 (April). Each call lasts approximately 20 seconds. Northern Saw-whet Owl (NSWO), Boreal Owl (BOOW), Barred Owl (BAOW), Long-eared Owl (LEOW), Great Grey Owl (GGOW)

Round 1	Round 2
2 min silence	2 min silence
NSWO	NSWO
1 min silence	1 min silence
NSWO	NSWO
1 min silence	1 min silence
NSWO	BOOW
1 min silence	1 min silence
BOOW	BOOW
1 min silence	1 min silence
BOOW	LEOW
1 min silence	1 min silence
BOOW	LEOW
1 min silence	1 min silence
BAOW	GGOW
1 min silence	1 min silence
BAOW	GGOW
1 min silence	1 min silence
BAOW	BAOW
3.5 min silence	1 min silence
tone beep	BAOW
	1 min silence
	BAOW
	1 min silence
	tone beep

all cases, as areas of land that are isolated from other forest patches by any area of a different land use type (Wiens 1976). I manually calculated the forest edge density to measure the amount of forest edge relative to total forest amount by dividing total forest-to-non-forest edges in each landscape by the total amount of forest in each landscape.

Configuration variables cover an almost endless list of measures of the spatial distribution of habitat on the landscape, many of which are highly correlated and redundant (McGarigal and McComb 1995). For the Alberta boreal mixedwood forest Vernier and Cumming (1998) divided configuration variables into seven categories: area, patch, edge, shape, core area, nearest neighbour, and contagion. These variables were then reduced to three principal components (uncorrelated linear combinations of the spatial metrics). A similar analysis was performed in the mainly coniferous forests of the west coast (McGarigal and McComb 1995) resulting in four principal components. I chose the following five configuration indices based on the principal component analysis from the studies mentioned above and an understanding of general raptor ecology (Table 2-5): Forest Edge Density, Forest Mean Patch Size, Forest Patch Size Variability, Forest Mean Nearest Neighbour, Forest Clumpiness (a measure of contagion). Total Core Forest Area was dropped from the list of configuration indices because it was highly linearly

Table 2-5. List of Configuration Metrics used, their definition, and implications for raptors.

Configuration Metric		Definition	Implications for owls
Forest Edge Density	**FED**	Meters of forest edge per square km of forest	Edge may function both as good hunting areas for large raptors and increased predation potential for small raptors.
Forest Mean Patch Size	**FMPS**	Total amount of forest/number of forest patches	Patch size may be important to nesting of some owl species.
Forest Patch Size Standard Deviation	**FPSSD**	Relative measure of the patch size variability	Along with Mean Patch Size may provide indication of a complex landscape with appropriate nesting patches (large) and foraging patches (small).
Forest Mean Nearest Neighbour	**FMNN**	A measure of the isolation of forest patches	May influence dispersal ability, foraging, territory size.
Forest Clumpiness	**FCLMP**	An index of the connectivity of forest patches in the landscape	May provide an indication of the permeability of the landscape to raptor movement.

correlated with percent forest cover and provided no additional information. Also of note, while the direction of most of the values is self evident (a high forest edge density value equals increasing edge), forest clumpiness may require some explanation. A high clumpiness value represents maximum aggregation of forest patches (suggesting low permeability across the landscape, because much of the forest area is aggregated in few areas), low clumpiness represents maximal disaggregation of forest patches (suggesting higher permeability across the landscape, as the forest cover is spread across many areas) (McGarigal *et al.* 2002).

Information theory

To address my objectives outlined in the introduction of this chapter I used an information-theoretic approach (see Burnham and Anderson 2002) with candidate models of various combinations of selected cover and configuration metrics. The models were compared and weighted according to the probability that they were the best-fit among the set of candidate models. I then repeated this information-theoretic approach using breakpoint regression to pinpoint potential threshold responses of owls to forest cover.

We used generalized linear models with Poisson or binomial errors, depending on the species. Poisson distributions were used for Great-horned Owls and Northern Saw-whets, while binomial distributions (presence/absence) were used for all other species due to low detection rates. The presence and abundance of species was calculated as the maximum abundance over the two survey rounds. I then created a combined dataset that included abundance data from Lac la Biche in 2002 and the maximum bird abundances over 2 years from Meanook and Ministik. All Statistical analysis was performed in S-plus 6.0 Professional Version.

Objective 1: Regional effects

Before I could begin addressing the linear responses of owls to forest cover and configuration I needed to determine whether or not there were regional differences in owl presences and abundance. I simply ran a generalized linear model with each species against region. Because region was significant for all species I then had to account for this factor in all other linear and breakpoint models. I did this by taking the residuals from the regional model and using them as the dependent variable in all other models.

Objectives 2 and 3: Linear models and relative importance of forest cover and configuration

To test the difference in owl response to forest cover and configuration I used generalized linear models to fit all residual species data (from the regional model described above) to a number of candidate models. The list of candidate models is outlined in Table 2-6. The first three linear models were designed to address my first question exploring the relative importance of forest availability versus forest configuration. Model 1, includes only Forest Cover while the second model, the full model with all possible parameters was:

Species Residuals~Region+ Forest Cover + FED + FMPS + FPSSD + FMPS:FPSSD + FMNN + FCLMP.

The 3rd model includes only the configuration variables. Interaction terms are represented with a colon between two or more parameters.

A step-wise regression was also included in the candidate set of models in place of any *a priori* hypothesis, due to the lack of information on the landscape scale habitat requirements of owls. The stepwise regression was performed in both directions

Table 2-6. List of models tested for each species. These models are designed to test Objectives 1 and 2. Parameters for the last three models are species specific, and are designed to address the importance of individual or groups of configuration metrics

Model #	Model Parameters	Rationale
Model 1	Forest	Forest cover
Model 2	Forest+FED+FPSSD+FMPS+FPSSD:FMPS+FMNN+FCLMP	Forest cover plus all configuration metrics
Model 3	FED+FPSSD+FMPS+FPSSD:FMPS+FMNN+FCLMP	All configuration metrics
Model 4	Values thought to be important for each species	Best-fit results from single year/region data*
Model 5	Values thought to be important for each species	Best-fit results from single year/region data*
Model 6	Species specific	Stepwise regression results

*see Appendix 1 for methods and results from this work

beginning with all possible parameters and parameters were then added or subtracted based on a Cp statistic. The Cp statistic is computationally related to the AIC such that $AIC = \sigma^2(Cp+n)$ (S-PLUS 2001). I also ran models for each year and study region and included best-fit models in the candidate set of models for this analysis (see Appendix). I considered my stepwise regression results plus the models taken from single year studies as a way of generating hypotheses for a system were there is very little information.

I used the Akaike Information Criterion (AICc) corrected to account for small sample sizes to compare the likelihood that each of the models was the most likely to be "true" of the set generated for each species. The AIC statistic was modified to AICc to account for sample sizes where: Sample Size - # Models < 40 (Burnham and Anderson 2002). The model with the highest Akaike weight (w_i) was selected as the best-fit model, as long as it was more than 3 times higher than the next highest weight (Burnham and Anderson 2002).

In cases where considerable model selection uncertainty existed (i.e. where no model fits the 3X rule described above) I used Akaike weights to estimate the relative importance of all parameters considered. The relative importance of each parameter was determined by summing the Akaike weights (w_I) for the subset of models that included each parameter. In this way I determined the relative importance of all variables whether they were included in the best model or not. This technique is especially valuable for hypothesis generation in systems where there is very little *a priori* knowledge (Burnham and Anderson 2002).

To help visualize the response of owls to forest cover relative to forest configuration I also created a Principal Component Analysis (PCA) Ordination. This analysis was performed in Multi-Variate Statistical Package (MVSP). The PCA was

calculated on all of the fragmentation indices described above, the data were centred around the origin of the graph, and the number of axis created were determined by Kaiser's Rule (Legendre and Legendre 1998). Data were also standardized, creating a correlation matrix, because all of the parameters in the analysis were of different units (MVSP 2002). I then created 3-D graphs, plotting species abundance (corrected for regional differences) against each PC axis and forest cover.

Objective 4: Breakpoint models and threshold responses to forest cover

To determine the best-fit threshold model I again developed a number of candidate models and compared them using AICc. Because regional affects were a concern for this dataset I again used only the residuals from the region model as the dependent variable in these models to remove regional effects. In this case, breakpoint generalized linear models (GLM) were developed with a defined breakpoint and separate slopes of the regression on either side of the breakpoint (Neter et al. 1985). In this way, a relationship was defined on either side of the breakpoint with the constraint that they met at the breakpoint. To model this breakpoint a second term was added to the GLM, the value of the term was calculated as 0 if the amount of forest cover in a landscape was less than the defined model breakpoint. If the amount of forest cover in the landscape was above that of the predetermined breakpoint the term was assigned a value of the difference between the two. I compared 11 breakpoint models with breakpoints at 5% forest cover intervals ranging from 10% to 60% forest cover because this was where I expected to see a breakpoint. This also ensured that there was enough data on both sides of the breakpoint to obtain model convergence. Model comparison was the same as for linear models. In cases where a single model fit the 3X criteria it was selected as the best-fit threshold model. Otherwise, I modified the rule such that the highest weighted

model PLUS the models on either side that were within the 3X rule were selected. This group of models represents the possible range of a threshold response.

In the case of the Barred Owl, where presences are sparse across years and regions, logistic regressions performed poorly. In some cases models would not converge at all, otherwise the predictive ability of the models was extremely low. In these latter cases, models were sometimes good at predicting Barred Owl absences, but the probability of accurately predicting presences was 0 or close to 0. For this species, I then calculated the percent of landscapes occupied by Barred Owls in forest class categories of 10%. I then ran a G-test on the entire table and on pairwise comparisons of two forest classes to determine which classes were significantly different from the others. For this analysis a p-value of .05 was considered significant.

RESULTS

Weather

In neither Round 1 nor Round 2 was there a significant correlation between temperature and forest cover (Round 1 R_s: 0.638, n = 143, Round 2 R_s: 0.804, n=143).

Owl detections

Table 2-7 outlines the number of detections by species across the entire study. Only Great-horned Owls, Northern Saw-whet Owls, and Barred Owls appeared in great enough numbers to perform statistical analysis and only these species are presented below in the results. Other species encountered during the surveys were excluded from the analysis due to a lack of detections.

Objective 1: Regional effects on the presence and abundance of owls

For all species there was a strong regional effect ($p < 0.001$) on the presence or abundance of owls (Table 2-8). However, the region that contributed most to this

regional effect was different for each species. Great Horned Owls had higher mean abundance at Ministik than Lac la Biche or Meanook. Much of this difference was apparent in the 2002 season, when Great Horned Owls were 1.6 times more abundant than the year before. Northern Saw-whet Owls were considerably less abundant at Lac la Biche versus the other two regions, and Barred Owls were most abundant at Meanook, with only a few presences in the other two regions.

Objective 2 and 3: Relative importance of changes in forest cover and configuration

Table 2-7. Number of detections by species over the entire study. Enough detections to perform analysis were acquired for only the first 3 species.

Species	Number of Detections
Northern Saw-whet Owls (NSWO)	529
Great Horned Owl (GHOW)	336
Barred Owl (BDOW)	31
Great Grey Owl (GGOW)	14
Long-eared Owl (LEOW)	11
Boreal Owl (BOOW)	8
Northern Hawk-owl (NHOW)	7
Northern Pygmy Owl (NPOW)	2
Unidentified (UID)	9

Table 2-8. Results of regional effects on all species. Region is significant for all species, $p \leq 0.001$. The mean abundance for each species in each region is presented, and the region contributing the most to regional differences is bolded.

			Regional Abundance Means		
Species	Model	*p*	Lac la Biche	Meanook	Ministik
Great Horned Owl	Region	<0.001	1.31	1.68	**3.84**
Northern Saw-whet Owl	Region	<0.001	**1.85**	3.08	3.82
Barred Owl	Region	<0.001	0.04	**0.28**	0.09

The PCA created two axes with eigenvalues >1 (variable loading for each axis is presented in Table 2-9), which, together accounted for 70.1% of the variation in the dataset. Axis 1 was correlated mainly with forest edge and patchiness. Landscapes that were associated positively with this axis had very small patches, with relatively high edge density, and patches were very far apart (high mean nearest neighbour) – being very highly fragmented. Landscapes negatively associated with this axis tended to have very large patches, relatively low edge density, and patches were very close together – being highly contiguous. Axis 2 is strongly correlated with connectivity (clumpiness), and patch size variation. Landscapes positively associated with this axis were composed of many patches that are highly connected and variable in size. Landscapes negatively associated with this axis had a few large patches that were very far apart, mainly of similar size, and connectivity was very low. Examples of landscapes representing the extremes of both axis are presented in the Appendix.

Great Horned Owls

The best-fit model for Great Horned Owls is Model #1 that included only forest cover (Table 2-10). The co-efficient for forest cover is slightly positive (0.016) indicating a positive relationship between Great Horned Owls and the amount of forest cover. All models in the candidate set have an R-squared less than 0.12, suggesting that none of them explain considerable variance in the dataset. Not unexpectedly, the more parameters in a model the higher the R-squared, though each parameter may only contribute to a small proportion of this value. The step-wise regression for Great Horned Owls produced Model #6 from Table 2-10, and only dropped one parameter: forest mean nearest neighbour, from the set.

Table 2-9. Two axes created by Principal Component Analysis to represent forest configuration. Together, these axes explain 70.1% of the variation. Axis 1 is heavily correlated positively with forest edge density (FED), forest mean nearest neighbout (FMNN) and negatively with forest mean patch size (FMPS). Axis 2 is heavily correlated negatively with forest clumpiness (FCLMP) and forest patch size standard deviation (FPSSD)

			Variable Loading				
Axis	Eigenvalue	Variation Explained (%)	FED	FPSSD	FMPS	FMNN	FCLMP
1	2.1	42.1	0.615	-0.281	-0.468	0.641	-0.175
2	1.4	28	0.343	0.434	0.127	-0.302	-0.766

Table 2-10. Great Horned Owl linear model comparisons. The best fit model is bolded, and must have an Akaike weight (wi) more than 3X higher than the next highest wi for sufficient evidence to support this model. The amount of variance explained by each model is represented by R^2. Interaction terms are represent by a colon between two (or more) parameters.

Model #	Model Parameters	AICc	wi	Multiple R-Squared
Model 1	***Forest**	**517.70**	**0.50**	**0.06**
Model 2	Forest+FED+FPSSD+FMPS+FPSSD:FMPS+FMNN+FCLMP	521.27	0.08	0.12
Model 3	FED+FPSSD+FMPS+FPSSD:FMPS+FMNN+FCLMP	522.76	0.04	0.09
Model 4	FED	521.97	0.06	0.03
Model 5	FPSSD	520.07	0.15	0.04
Model 6	Forest+FED+FPSSD+ FMPS+FCLMP+FPSSD:FMPS	519.90	0.17	0.11

Table 2-11. Relative importance of all parameters in all models for Great Horned Owls. This analysis estimates the relative importance of each parameter relative to one another. This technique is especially valuable for analysis in systems where there is very little *a priori* information. Total relative importance of each parameter is calculated by adding the weight (wi) of all models in which it appears (i.e. has a value of 1).

Model #	Forest	FED	FPSSD	FMPS	FPSSD:FMPS	FMNN	FCLMP	*wi*
1	1	0	0	0	0	0	0	0.50
2	1	1	1	1	1	1	1	0.08
3	0	1	1	1	1	1	1	0.04
4	0	1	0	0	0	0	0	0.06
5	0	0	1	0	0	0	0	0.15
6	1	1	1	1	1	0	1	0.17
Relative Importance:	**0.75**	**0.35**	**0.44**	**0.29**	**0.29**	**0.12**	**0.29**	

In the comparison of the relative importance of all parameters (Table 2-11) forest cover again appears as the most important parameter, though all parameters rank high. This suggests that while Forest Cover may be the most important for Great Horned Owls, configuration metrics may also have an influence on species abundance as well.

Great Horned Owls were also more likely to be found, overall, in landscapes with relatively low fragmentation (represented by Axis 1 from the PCA) and moderate amounts of forest cover. Similarly, they are also more abundant when connectivity is moderately high, and forest cover is moderate (Figure 2-3).

Northern Saw-whet Owls

The best-fit model for Northern Saw-whet Owls was also Model #1: forest cover, with the relationship between species abundance and the amount of forest cover being slightly positive (co-efficient = 0.008) (Table 2-12). This model accounted for only 2% of the variation in the dataset and had a *wi* of 0.47, which did not meet the 3X rule, suggesting there is not enough evidence to conclude that this is the best model of the set. All models in the candidate set have R-squared values equal or less than 0.05, suggesting no model can explain substantial amount of the variation in the dataset.

In examining the relative importance of all parameters, forest cover ranked the highest, supporting the results from the model comparison (Table 2-13). Forest mean patch size and forest patch size standard deviation are also relatively important, with both of these relationships being generally slightly negative.

Northern Saw-whet Owls did not respond strongly to either forest fragmentation or forest cover, though their abundance dropped off significantly when forest cover reached extreme lows and forest fragmentation (axis 1) was very high (Fig. 2-4a). As

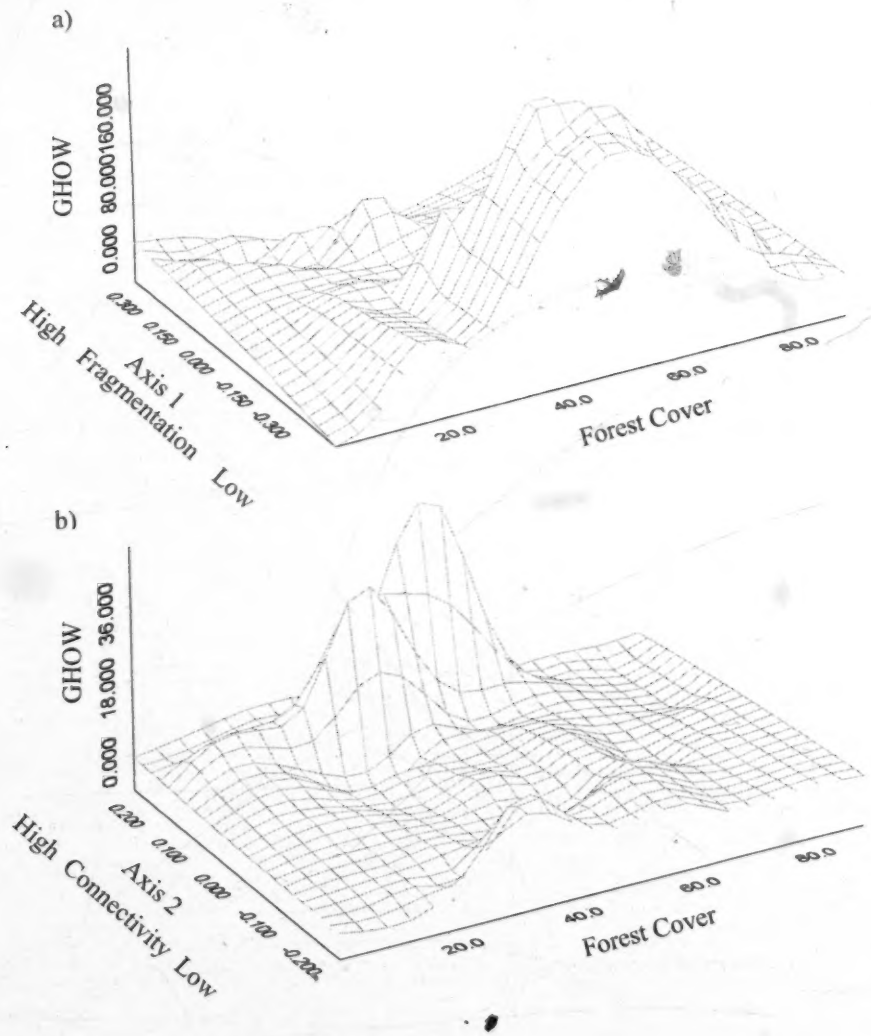


Figure 2-3. 3-D plots of Great Horned Owls (corrected for regional variation) against a) Axis 1 (fragmentation) and forest cover, b) Axis 2 (connectivity) and forest cover.

Table 2-12. Northern Saw-whet Owl linear model comparisons. The best fit model is bolded, and must have an Akaike weight (wi) more than 3X higher than the next highest wi for sufficient evidence to support this model. The amount of variance explained by each model is represented by R^2. Interaction terms are represent by a colon between two (or more) parameters.

Model #	Model Parameters	AICc	wi	Multiple R-Squared
Model 1	**Forest**	**479.15**	**0.47**	**0.02**
Model 2	Forest+FED+FPSSD+FMPS+FPSSD:FMPS+FMNN+FCLMP	487.33	0.01	0.05
Model 3	FED+FPSSD+FMPS+FPSSD:FMPS+FMNN+FCLMP	485.18	0.02	0.05
Model 4	FPSSD	481.31	0.16	0.00
Model 5	Forest+FMPS	480.03	0.30	0.03
Model 6	Forest+FED+FPSSD+FMPS+FPSSD:FMPS	483.96	0.04	0.04

Table 2-13. Relative importance of all parameters in all models for Northern Saw-whet Owls. This analysis estimates the relative importance of each parameter relative to one another. This technique is especially valuable for analysis in systems where there is very little *a priori* information. Total relative importance of each parameter is calculated by adding the weight (wi) of all models in which it appears (i.e. has a value of 1).

Model #	Forest	FED	FPSSD	FMPS	FPSSD:FMPS	FMNN	FCLMP	*wi*
1	1	0	0	0	0	0	0	0.47
2	1	1	1	1	1	1	1	0.01
3	0	1	1	1	1	1	1	0.02
4	0	0	1	0	0	0	0	0.16
5	0	0	0	1	0	0	0	0.30
6	1	1	1	1	1	0	0	0.04
Relative Importance:	**0.52**	**0.07**	**0.23**	**0.37**	**0.07**	**0.03**	**0.03**	

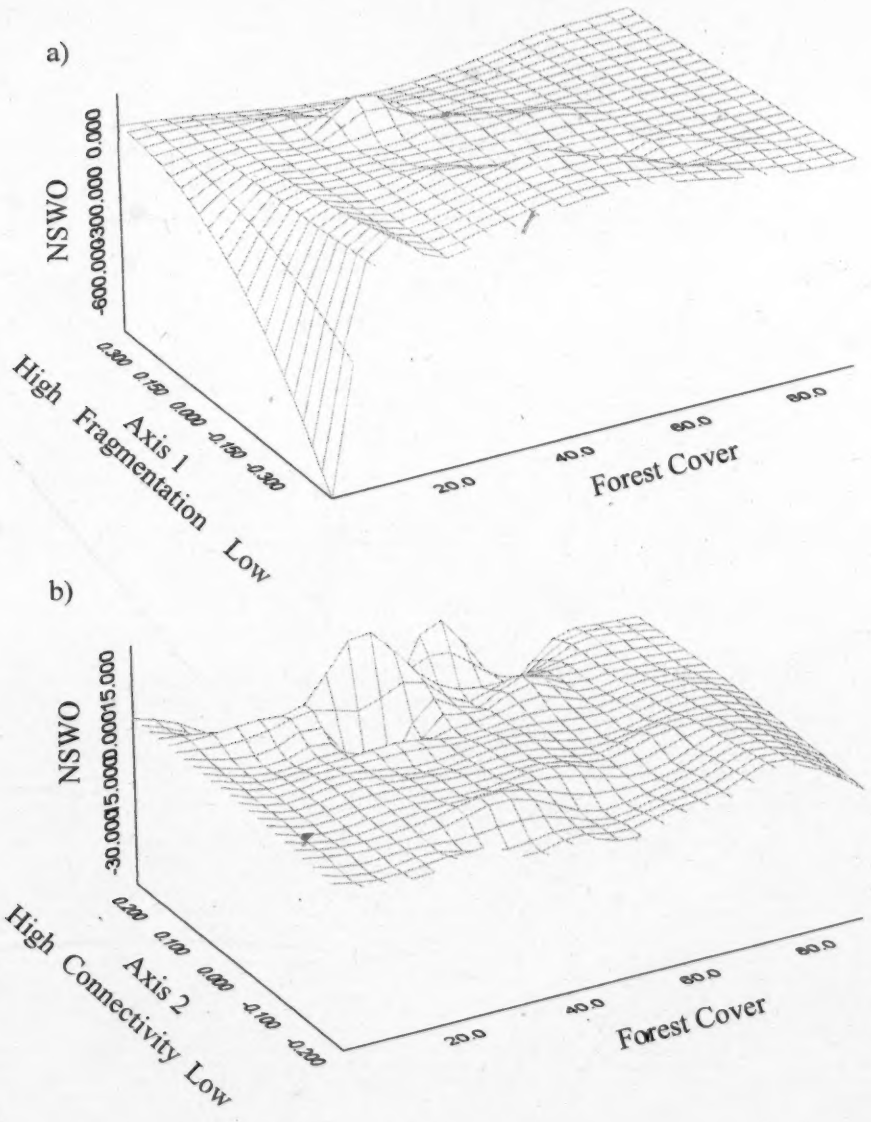


Figure 2-4. 3-D plots of Northern Sawwhet Owls (corrected for regional variation) against a) Axis 1 (fragmentation) and forest cover, b) Axis 2 (connectivity) and forest cover.

well, they were most likely to be found when forest cover was moderate and connectivity through the landscape was high (Fig. 2-4b).

Barred Owls

Two models, Model 1 (Forest Cover) and Model 6 (FMPS + FPSSD) are equally likely to be the best-fit model in the set for Barred Owls (Table 2-14). This strongly suggests that no model in the set can confidently be selected as the best fit. Both models explain 12% of the deviance in the dataset, with the highest deviance (16%) being explained in Model 3 (all configuration variables). In an examination of the relative importance of all the parameters Forest Mean Patch Size may be the most important of the three parameters included in the best-fit models, with Forest Patch Size Coefficient of Variation and Forest Cover approximately equally placed behind it (Table 2-15). Barred Owl abundance was variable across a range of forest fragmentation (Axis 1), though they were most likely to be found in landscapes with very high connectivity when forest cover was moderate. When forest cover was higher, they were found most often in landscapes with moderate connectivity (Fig. 2-5).

Objective 4: Threshold responses to changes in habitat availability and configuration

Clear threshold responses to forest cover were apparent only for Great Horned Owls. Barred Owls may have had a weak threshold response at approximately 45% to 60% forest cover, while Northern Saw-whet Owls appear to have had no threshold response at all.

Great Horned Owl

Table 2-14. Barred Owl linear model comparisons. The best fit model is bolded, and must have an Akaike weight (wi) more than 3X higher than the next highest wi for sufficient evidence to support this model. The amount of variance explained by each model is represented by R^2. Interaction terms are represent by a colon between two (or more) parameters.

Model #	Model Parameters	AICc	wi	Deviance Explained
Model 1	**Forest**	**174.06**	**0.34**	**0.12**
Model 2	Forest + FED + FPSSD + FMPS +FPSSD:FMPS + FMNN + FCLM	183.19	0.00	0.14
Model 3	FED + FPSSD + FMPS +FPSSD:FMPS + FMNN + FCLMP	180.79	0.01	0.16
Model 4	FED	181.85	0.01	0.04
Model 5	FMPS	174.27	0.30	0.09
Model 6	**FMPS+FPSSD**	**174.04**	**0.34**	**0.12**

Table 2-15. Relative importance of all parameters in all models for Barred Owls. This analysis estimates the relative importance of each parameter relative to one another. This technique is especially valuable for analysis in systems where there is very little *a priori* information. Total relative importance of each parameter is calculated by adding the weight (wi) of all models in which it appears (i.e. has a value of 1).

Model #	Forest	FED	FPSSD	FMPS	FPSSD:FMPS	FMNN	FCLMP	*wi*
1	1	0	0	0	0	0	0	0.34
2	1	1	1	1	1	1	1	0.00
3	0	1	1	1	1	1	1	0.01
4	0	1	0	0	0	0	0	0.01
5	0	0	0	1	0	0	0	0.30
6	0	0	1	1	0	0	0	0.34
Relative Importance:	**0.34**	**0.02**	**0.36**	**0.66**	**0.02**	**0.02**	**0.02**	

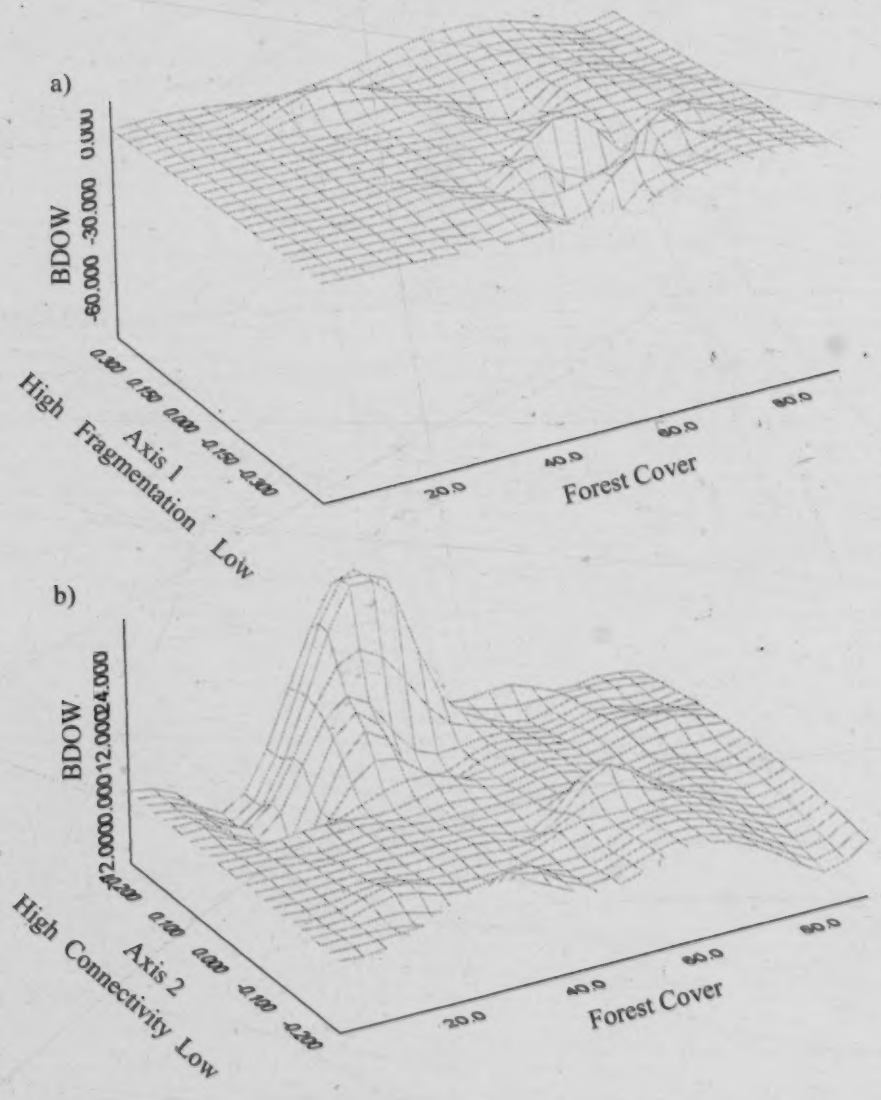


Figure 2-5. 3-D plots of Barred Owls (corrected for regional variation against a) Axis 1 (fragmentation) and forest cover, b) Axis 2 (connectivity) and forest cover.

A threshold response at 60% forest cover is the best-fit model for Great Horned Owls (Table 2-16). This model, with an AICc weighting of 47%, passed the 3X rule and was selected as the best model of the set. This model has a Multiple R-squared value of 0.07. The linear forest cover model has a wi of only 4% and has a Multiple R-squared value of 0.06. The probability of fit for a threshold model declines markedly below 60% forest cover.

Northern Saw-whet Owl

No threshold model is apparent for Northern Saw-whet Owls (Table 2-16). The linear Forest Cover model is the best-fit of the set, with a *wi* of only 19%, explaining 12% of the variation in the dataset. All threshold models with the exception of Model 2 (threshold = 10% forest cover) have the same *wi*, suggesting that all models are equally good (or bad) fits to the data.

Barred Owl

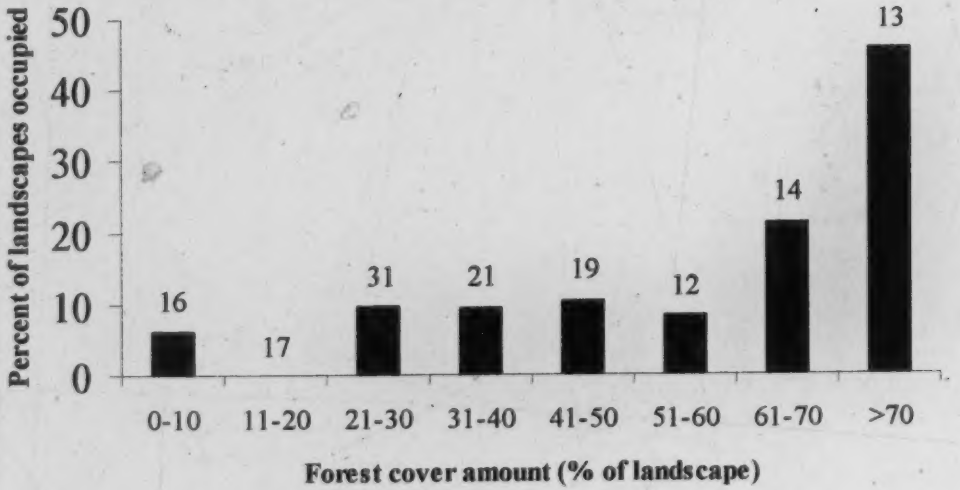
No breakpoint model for Barred Owls met the 3X rule, suggesting that no threshold exists. A range of possible thresholds may exist between 45% and 60% forest cover (representing the range of breakpoint models within the 3X rule for the best fit), however the evidence for this is slight.

From the G-test analysis the percent of landscapes occupied in 60 – 70% forest cover and >70% forest cover are not significantly different ($G = 1.76$, $p = 0.18$). However, the percent of landscapes occupied in this highest level of forest cover is significantly different from all other forest classes (see Figure 2-6). This may represent a threshold response of presence on the landscape at 60% forest cover.

Table 2-16. Best fit breakpoint models for all species. Only Great Horned Owls have a single model that meets the 3X criterion described above. For Barred Owls the best fit model is presented (in bold) along with the surrounding models that are within the 3X rule – suggesting a possible threshold range.

Species	Best-fit Threshold	AICc	*wi*	Variance/ Deviance Explained
Great Horned Owl	**60**	**512.35**	**0.46**	**0.07**
Northern Saw-whet Owl	N/A	N/A	N/A	N/A
Barred Owl	45	170.61	0.13	0.17
	50	169.75	0.21	0.17
	55	**169.61**	**0.22**	**0.17**
	60	170.04	0.18	0.16

Figure 2-6. Percent of landscapes occupied by Barred Owls per forest cover class. Only class 61% - 70% was not significantly different from class >70. This may represent a threshold of Barred Owl presences on the landscape when forest cover falls below 60%. This result is similar to that from the breakpoint regression analysis.



DISCUSSION

Weather effects

In Chapter 3 I discuss the effects of a number of weather parameters on my ability to detect Great Horned and Northern Saw-whet Owls. The detection of both species was affected by a number of weather and time variables. However, I was able to control for the vast majority of these variables (see the part on winter nocturnal owl surveys in the methods section) through my experimental design. Only temperature was not specifically controlled for, and appeared as a factor for both species and as an interaction with forest cover for Northern Saw-whet Owls. However, temperature and forest cover were not correlated in this analysis, so we can rule out the possibility weather effects confounded the analyses presented in this chapter.

Regional effects on owl presence and abundance

Of the three regions surveyed in this study Lac la Biche had the highest percentage of its landscape in forest cover, at 55%. Meanook followed with 45% forest cover and Ministik had only 25% of its landscape in forest. Other outstanding differences between these regions are that Lac la Biche had considerably more wetland areas than either other landscapes, and also had some clearcuts (the others have minimal or no clearcuts); also Ministik had a large proportion of its landscape in crop or pasture, which sets it apart from both Meanook and Lac la Biche (Table 2-1).

Based on the regional differences described above I expected that Barred Owls would be more abundant at Lac la Biche, where there is considerable contiguous forest habitat and that Northern Saw-whet Owls and Great Horned Owls would be more abundant at a Meanook, where there is a moderate amount of habitat fragmentation.

Regional effects were strong for all species, though the region contributing to this effect is different for each species. These regional differences may be in response to differences in land uses at this scale. Great Horned Owls may be keying into regional forest cover, as it was highest at Ministik and this region varies from the other two

Northern Saw-whet Owls were least abundant at Lac la Biche (where forest cover was the highest and there is considerable wetland habitat) and were approximately equally abundant at Meanook and Ministik. While there is very little known about the habitat associations of Northern Saw-whet Owls, there is some evidence to suggest they prefer complex landscapes, and may be using forest interspersed with open habitat for multiple functions (hunting, nesting, roosting, etc.).

While it was expected that Barred Owls would be most abundant at Lac la Biche they were in fact, most abundant at Meanook and least abundant at Lac la Biche. Lac la Biche may be less desirable for Barred Owls despite its relatively high proportion of contiguous forest because of the high wetland component. These wetlands may represent unfavourable open habitat for a species that hunts and nests mainly in interior forest habitat

Owls responded to regional differences, but the nature of these differences between regions was unclear. Meyer *et al.* (1998) found that Spotted Owl presence was most strongly influenced by habitat characteristics within an area of 0.8 km and less strongly by an area of 3.4 km. Similarly, Swindle *et al.* (1999) found that Spotted Owls were responsive mainly to habitat characteristics within 200m of a nest site, and decreasingly so as distance from the nest increased. I have found no other research that examines the influence of regional differences at this scale on owl populations. This suggests that owls may be selecting nest sites based on small-scale habitat characteristics

in the immediate vicinity of a potential nest, but species abundance may be more influenced by large regional scale habitat characteristics. Given the importance of regional factors on owl populations, research into determining the source of these differences may be crucial to getting a handle on the population trends and dynamics of this poorly understood taxon (Kirk 2003).

Many studies from work on songbirds have corroborated the importance of regional landscape context on bird populations (McGarigal and McComb 1995, Pearson 1993, Hansen and Urban 1992, Lee *et al.* 2002). As well, numerous authors have found the amount of forest cover regionally to be the most significant influence on bird abundance (Askins and Philbrick 1987, McGarigal and McComb 1995, Trzcinski *et al.* 1999, and Howell *et al.* 2000). Regional habitat characteristics may be important to songbirds because factors that affect bird productivity, e.g. nest predation and cowbird abundance, may be related to habitat fragmentation at the regional scale (Donovan *et al.* 1997). While nest parasitism may not be particularly important for many owl species that breed too early for cowbirds, the abundance of nest predators would be of concern. Many of the same species that commonly predate songbird nests, e.g. corvids and small mammals, may be culprits in the failure of owl nests as well (Overskaug *et al.* 1999, Sonerud 1985).

In contrast to these findings, Jokimaki *et al.* (2000) and Jones *et al.* (2000) suggest that local habitat structure may be more important for generalist species not restricted to specialized habitat characteristics. This may be because habitat heterogeneity at fine scales provides important foraging/hunting opportunities. Similarly, Lichstein *et al.* (2002) suggested that while some neo-tropical migrants respond to habitat

composition and pattern at the regional level, these variables explain only a small amount of the variation in local population abundances.

Linear responses to forest cover and configuration

All of the owl species I examined responded most strongly to the amount of forest in the landscape, however, only in the case of the Great Horned Owl is the response strong. Forest edge density and forest patch size standard deviation were also important. Great Horned Owls are associated with open non-forest habitats (James and Neal 1986, Johnson 1993, and Morrell and Yahner 1994). However, the results of this analysis show that they respond slightly positively to increasing forest cover and slightly negatively to forest edge density. This suggests that while they use forest edges extensively for hunting (Bosakowski *et al.* 1989 and Rohner and Krebs 1996), they certainly require some forest for nesting and prefer slightly lower forest edge density (forest edge density co-efficient: -0.002). This result is also reflected in the PCA, where owls were most abundant at relatively high forest cover, with low to moderate fragmentation. Possibly, Great Horned Owls respond to forest cover and forest edge density in a quadratic way, reaching highest abundance at moderate levels of these parameters. The PCA also suggests this possible quadratic relationship, with few birds at either extreme of forest cover, and the majority at moderate levels of forest cover (both on Axis1 and 2).

The amount of forest and forest edge was important for Great Horned Owls, whose prey base in Alberta is mainly snowshoe hares (*Lepus americanus*) and small mammals. Snowshoe hares select for forested habitats and avoid open areas (St. Georges *et al.* 1995, MacCracken *et al.* 1988), though they may be more vulnerable to predation at forest edges or in small patches (Rohner and Krebs 1998, Keith *et al.* 1993). Similarly, the preferred prey alternative to snowshoe hares, field voles (*Microtus*), prefer open

habitat (Boonstra *et al.* 2001). A moderate amount of forest edges, then, may provide excellent perches for Great Horned Owls to forage in open fields or clearings.

For Northern Saw-whet Owls, the amount of forest cover has the highest Akaike weighting of the set, but the evidence for this model confidently being selected as the best model was weak. However, forest cover was the most important of all variables, with forest mean patch size and patch size standard deviation also appearing as relatively important parameters with a slightly negative response. This suggests that Northen Saw-whet Owls prefer landscapes with relatively high forest cover, and many small patches. This may reflect a preference for complex forested landscapes with many small patches to facilitate hunting along forest edges, and minimizing predation from other owls, but also providing dense shrubby habitat for roosting (Cannings 1993). However, Northern Saw-whet Owl abundance did not vary considerably across a range of forest fragmentation and forest cover (Fig. 2-4a), but were more responsive to variation in forest connectivity and patch size. This further suggests a preference for highly complex landscapes with patches of variable sizes that are dispersed across a landscape.

The Queen Charlotte Island Northern Saw-whet Owl (*Aegolius acadicus brooksi*) tends to prefer habitat that incorporates some old forest, some young forest, and some open area – suggesting a preference for heterogeneous landscapes (Gill and Cannings 1997). Unfortunately, there is very little detailed information is available regarding the habitat selection of this species or other congenerics – which may share some habitat associations (Hayward and Hayward 1993). Some information from the Tengmalm's Owl in Europe (*Aegolius funereus*) suggests that predator/prey dynamics is the most important factor influencing habitat selection (Hakkarianen *et al.* 1997). An examination of the home range of a single bird revealed a inclination towards forested landscapes with

some open areas (Sonerud *et al.* 1986). These birds also tend to hunt along forest edges of clear-cuts or fields (Korpimaki 1988). In North America the Boreal Owl is the more northerly counterpart to the Northern Saw-whet Owl, inhabiting mainly spruce and fir forests, and hunting in both forest interiors and edges (Bondrup-Nielson 1978, Palmer 1986, and Hayward *et al.* 1987, Hayward *et al.* 1993).

Barred Owl presence is predicted mainly by the amount of forest cover, followed by a combination of forest mean patch size and forest patch size standard deviation. Barred Owls may prefer landscapes with large patches for nesting, containing smaller patches for hunting, though the species is suspected to hunt mainly in mature forest areas (Mazur et al. 1998). Highly connected landscapes may provide optimal hunting opportunities for Barred Owls, allowing them to move across a large area easily through a well-connected forest network. Olsen (1999) and Takats (1998) have examined the habitat associations of Barred Owls in Alberta. Barred Owls preferred mixedwood forests with access to water (this connection to water may be related to the presence of older trees with critical nesting snags along waterways), and a tendency to select mature to old forests. Barred Owls in the boreal forest of Saskatchewan also select mature forests (Mazur *et al.* 1998), and this pattern is evident in western Newfoundland as well (Gosse and Montevecchi 2001).

Evidence for habitat associations similar to the Barred Owl from related species comes from the Spotted Owl, *Strix occidentalis* (a North American congeneric) and the Tawny Owl, *Strix aluco* (a European congeneric). Considerable work has been done on the endangered Northern Spotted Owl in western North America, suggesting it is, like the Barred Owl, tied to mature, contiguous forests. Site selection by Spotted Owls is also dominated by the amount of habitat on the landscape and the size of old-growth patches

(Meyer et al. 1998). Both Spotted Owls and Barred Owls appeared to be abundant in areas with similar habitat qualities, and are responsive to both habitat availability and configuration. In another study, however, Spotted Owls appear to respond negatively to the amount of forest and positively to forest edge – which may provide excellent foraging opportunities (Franklin *et al.* 2000).

Threshold responses to forest cover

Threshold responses were only apparent for Great Horned Owls and Barred Owls, though there was only strong evidence for the former. Both of these species show threshold responses between 45% and 60% forest cover, at the higher end of that expected from Andren's (1994) analysis. The threshold model for Great Horned Owls, though it was a better fit than the linear forest cover model, did not explain as much variation, possibly because the Great Horned Owl may have a quadratic response to forest cover. Only the range of threshold models for the Barred Owl explained more variation than a linear model, though there is not enough evidence to support these models as a best-fit of the set. This suggests that the presence of a biologically significant threshold response to changes in habitat availability was unlikely, or that I was unable to detect a significant threshold response due to low sample sizes and high annual and regional variability. Northern Saw-whet Owls did not exhibit a threshold response to forest cover.

Conclusions

Linear relationships between owl presence and abundance and landscape level forest cover and configuration were quite weak. However, all species were responsive to the amount of forest cover in the landscape, suggesting that the amount of habitat available was more important to owl populations than the configuration of that habitat.

These results confirm numerous other studies of a similar nature on songbird population responses to habitat availability and configuration. Forest edge density and forest patch size and standard deviation may be other important configuration parameters influencing owl populations.

There is, importantly, considerable evidence to suggest that regional habitat characteristics may also be critical to determining owl populations at the landscape level. Determining the habitat associations of owls at this scale may be the next critical step to developing appropriate management plans for this taxon. Threshold responses to landscape level habitat characteristics are clear only for the Great Horned Owl.

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CHAPTER 3

Effects of weather, time of day and season on the detection of owls

INTRODUCTION

The effects of uncontrollable and unpredictable weather conditions invariably complicate surveying animals in the wild. In many cases, these weather conditions can affect detectibility, (e.g., precipitation causing poor visibility for visually monitoring species) or animal behaviour (e.g., individuals becoming less active during extreme temperatures). It is critical to understand and account for these confounding variables in any study of wild animals.

Owls are a group of birds that typically endure extreme winter weather conditions in Alberta. Weather during their peak breeding (and censusing) time can fluctuate from nightly temperature lows of -35° to +15°, with winds ranging from 0 to 50 km/h (Grossman pers. obs). These conditions could affect my ability to accurately survey owl populations. Weather is known to influence the detection of owl species. In Alberta, Takats (1998) found that Barred Owl detections were influenced by both moon phase and temperature. Other researchers have found wind and temperature to affect detection of owls. Elf Owls (*Micrathene whitneyi*), Western Screech Owls (*Otus kennicottii*) and Mottled Owls (*Strix virgata*) are detected more often when winds are relatively light (Hardy and Morrison 2000, Gerhardt 1991). The influence of weather may be species-specific, e.g. Elf Owls were affected by wind and moonlight and Western Screech Owls by wind, temperature and cloud cover (during the same study) (Hardy and Morrison 2000). In contrast, Redpath (1994) found that no weather variables had any impact on the detection of Tawny Owls.

In this chapter I present data on the effect of temperature, wind, moon visibility, time of evening, and time of year, as well as wind and temperature interactions with forest cover on the detection of Great Horned Owls and Northern Saw-whet Owls in Alberta. Wind interactions with forest cover are likely, given the potential for wind to create more background noise through trees. Also, temperature may vary with forest cover, as interior forest areas may be insulated from extreme temperature variation and high winds (Burke and Nol 1998, Chen *et al.* 1995).

RESEARCH METHODS

Study area

This study was conducted in 3 regions across east-central Alberta: Ministik, **MSTK** (53°38'N 112°50W); Meanook, **MNK** (54°33'N 113°20'W); and Lac la Biche **LLB** (54°24'N 112°6'W) (Fig. 2-1). All three of these regions were 12,600 km^2 and were located within the transition zone between Aspen (*Populus tremuloides*) forests to the south and boreal forests to the north.

Experimental design

A brief description of the research methods is outlined here; for a more detailed discussion of the methods see Chapter 2. Within each of the 3 study regions 45 to 50 landscapes, each approximately 3 by 5 km, were chosen to represent a gradient in forest cover. Landscapes were spaced at least 2km apart to avoid sampling the same individuals in 2 different plots.

Winter nocturnal owl surveys

Owls were monitored using a playback technique, where recordings of conspecific owl calls were used to elicit responses from territorial birds. Before beginning owl surveys I calibrated the volume of the CD player to control for the

difference in the transmission of sound in landscapes with varying degrees of forest cover. Five broadcast stations were set up in each landscape to survey owls (Fig. 3-1). These stations were separated by 1.6 km, a distance slightly greater than the maximum distance an owl call could be detected (Bondrup-Nielsen 1984). Surveys were conducted in 2 rounds, with Round 1 lasting from mid February to the end of March, and Round 2 lasting to the end of April. In Alberta the peak owl breeding season begins in mid February and continues through to the end of April, (Johnsgard 1988) and owls are most vocal during this period.

One to two observers conducted owl surveys beginning 30 minutes after sunset and continuing for a maximum of 8 hours, playing a CD recording of vocalizations of expected owl species (see Table 3-1 for a list of expected owl species, and the play list). The playback CDs were designed with 20 – 30 second recordings of owl calls interspersed with 1-minute periods of silence. Long-eared Owls (*Asio otus*) and Great Grey Owls (*Strix nebulosa*) were not included on the tapes until the second round because they breed later than other species in central Alberta (Olsen 1999). The Great-horned Owl was excluded from the tapes due to its propensity to respond to the call of hetero-specifics (Bosakowski and Smith 1998) and the possibility its call could reduce the response rate of other owl species it preys upon. During the first round I played each call being once in each of three directions (N, ESE, and WSW) to elicit responses from nearby owls at each broadcast station. In the second round all landscapes were surveyed again and the order of the stations was reversed. After recording the estimated distance

Figure 3-1. Landscape design with 5 broadcast points. Playback surveys were conducted at each broadcast point in 2 rounds. Each point surveys a radius of approximately 700m.

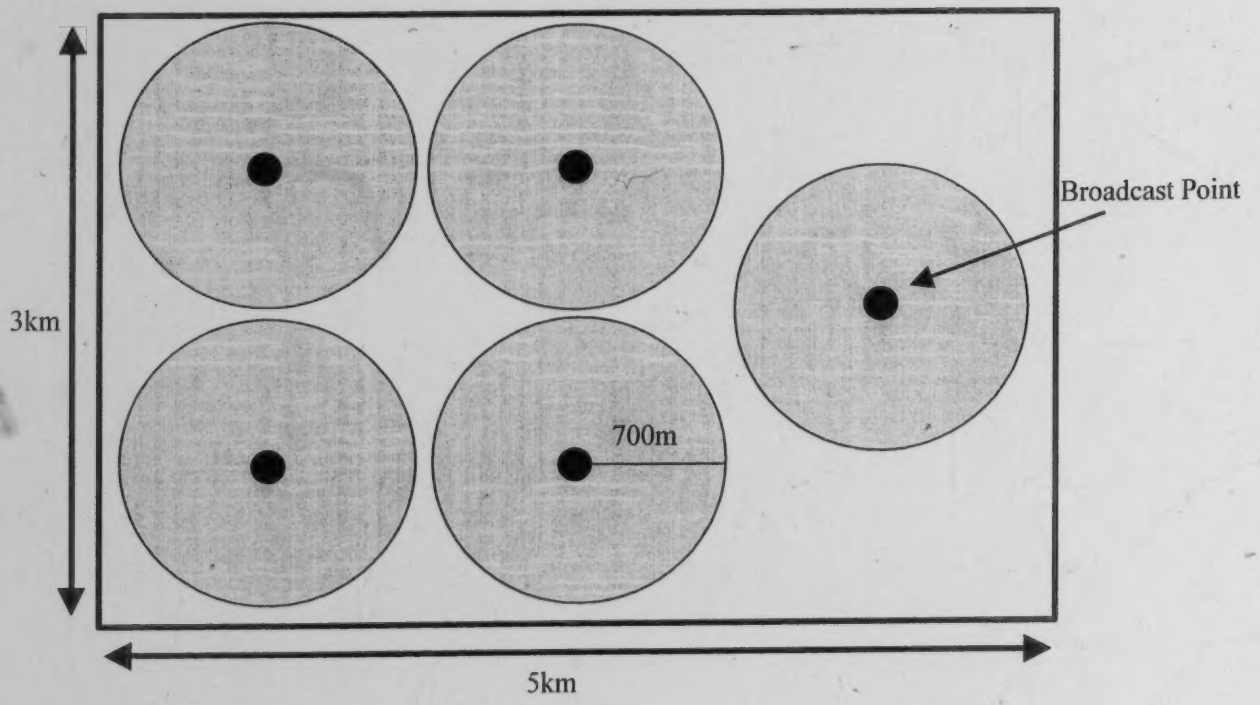

Table 3-1. Play list for owl surveys CDs for Round 1 (Feb-March) and Round 2 (April). Each call lasts approximately 20 seconds. Northern Saw-whet Owl (NSWO), Boreal Owl (BOOW), Barred Owl (BAOW), Long-eared Owl (LEOW), Great Grey Owl (GGOW)

Round 1	Round 2
2 min silence	2 min silence
NSWO	NSWO
1 min silence	1 min silence
NSWO	NSWO
1 min silence	1 min silence
NSWO	BOOW
1 min silence	1 min silence
BOOW	BOOW
1 min silence	1 min silence
BOOW	LEOW
1 min silence	1 min silence
BOOW	LEOW
1 min silence	1 min silence
BAOW	GGOW
1 min silence	1 min silence
BAOW	GGOW
1 min silence	1 min silence
BAOW	BAOW
3.5 min silence	1 min silence
tone beep	BAOW
	1 min silence
	BAOW
	1 min silence
	tone beep

and direction of owl responses, I then scanned the area with a high-powered flashlight to locate birds that came in to the playbacks but did not vocalize.

At each site I recorded weather conditions including temperature, wind (using the Beaufort scale), cloud cover (percent of sky in cloud), moon phase (based on 8 phases), moon visibility (percent of moon visible), precipitation, and snow cover (average centimeters on ground). Owl surveys were not conducted in high winds (≥3 on the Beaufort scale), or if there was considerable rain or snow.

Data analysis

Moon Phase was categorized from 8 original moon phases to 3 based on the amount of light that each phase was expected to give. A new moon and both waxing and waning quarter moons were considered low light, and given a value of 1. A waxing and waning half moon, plus a waning ¾ moon were considered moderate light, and given a value of 2, while a full and waxing ¾ moon were considered high visibility and a value of 3. Moon visibility was defined as the percent of the moon expected to be visible (given its phase) that was actually visible, i.e., not clouded over. I combined these two values to create a visibility index: Moon Phase * Moon Visibility. This variable gave a relative estimate of the visibility over an evening and ranged from 0 to 300. Time was also categorized into 3 time slots based on the time from sunset: 1 = 0 – 3 hours after sunset, 2 = 3 – 6 hours after sunset, 3 = and 6 – 8 hours after sunset. I used Julian calendar day (1 – 365) to represent the time of year. I also included interactions between temperature and forest cover, because the ambient temperature may be affected by the amount of forest on a landscape (Chen *et al.* 1995); and wind and forest cover, because the increased noise created by wind blowing through trees may affect observer ability to detect owls. Similarly, forests may act as a buffer for wind, such that the more forest on

a landscape the more buffer there may be for high winds. For all weather data I selected the median value for each landscape to represent the general weather conditions for that survey.

We compiled data from all three regions from 2002. For landscapes where owls were detected in either Round 1 or Round 2 I subtracted owl abundance in Round 1 from Round 2. The same manipulation was performed on the weather data to create a matrix of the differential weather and owl abundances for each landscape over the two rounds. This allowed me to compare the response rate of owls at a single location under different weather and time conditions.

Statistical analysis was performed with a stepwise linear regression in both directions (normal distribution). The full model was run and then parameters were added or dropped based on a Cp statistic. The Cp statistic is computationally related to AIC; such that AIC = σ^2(Cp+n) (S-PLUS 2001). Abundance differences for each species were run against all weather variables, forest cover and interactions between forest cover and temperature and forest cover and wind speed.

RESULTS

Seven owl species were recorded in all landscapes sampled in 2002, however, I only had enough detections for Great Horned Owls and Northern Saw-whet Owls to perform adequate analysis. Only results for these species are presented below. Great Horned Owls were more likely to be detected in low forest cover, at warmer temperatures, lower wind speeds, and later in the evening (Table 3-2). Northern Saw-whet Owls were more likely to be detected in high forest cover, low temperatures, earlier in the season, and when both temperature and forest cover are high.

Table 3-2. Linear regression models describing the influence of weather, timing, and season on the detection of Great Horned Owls and Northern Saw-whet Owls. All parameters represent the difference between Round 1 and Round 2 at a single landscape. F = Forest Cover, T = Temperature, TY = Time of Year, FT = Forest:Temperature Interaction, W = Wind, TE = Time of Evening, and FW = Forest:Wind Interaction.

Species	Model	*p*	F	R^2
GHOW	-0.508 – 0.02F + 0.068T – 1.495W + 0.582TE + 0.018FW	<0.01	3.505	0.1835
NSWO	-2.675 + 0.034F – 0.018T – 0.041TY + 0.002FT	<0.001	7.813	0.2152

DISCUSSION

Weather affected the detection of owls in Alberta, and the importance of individual weather parameters was different for each species. Temperature was significant for both Great Horned Owls and Northern Saw-whet Owls in central Alberta, but this is the only weather variable they commonly responded to. Interestingly, the relationship between temperature and owl detection was positive for Great Horned Owls and negative for Saw-whet Owls. Great Horned Owls may expend less energy on territory defence and calling on colder nights to conserve energy. Northern Saw-whet Owls are quite small birds and may be expected to become less active in cold temperatures than the large bodied Great Horned Owl. However, they may also be using a niche separation along the temperature gradient to avoid predation from Great Horned Owls during warmer nights when their predators are more active.

The importance of both wind and temperature on owl detections is consistent with other research on various owl species. Western Screech Owls and Mottled Owls are both less likely to be detected when winds are high (Gerhardt 1991, Hardy and Morrison 2000). Western Screech Owls, along with Barred Owls, have also been found to call less when temperatures drop (Hardy and Morrison 2000, Takats 1998), Great Horned Owl detections similarly, had a positive response to temperature in this study.

Not unexpectedly, wind had a strong negative relationship on Great Horned Owl detection. This likely reflects the reduced sound transmission when winds are high, rather than a predilection for owls to be less active when it is windy. This is especially likely because I only surveyed for owls when winds were relatively light (Beaufort 3, <20km/h). The Wind/Forest interaction may also reflect the increased noise in forested areas from wind blowing through branches (Grossman, pers. obs.). Also of note is that

Great Horned Owls are detected more often in late evenings rather than earlier in the night. This may suggest that surveying for this species is most efficient between 6 and 9 hours after sunset.

Conclusions

As expected, weather influenced the detection of owls in central Alberta. Temperature was the only weather variable that both Northern Saw-whet Owls and Great Horned Owls responded to. There was species specific variation in the response to weather variables, with Northern Saw-whet Owls responding to Time of Year and a Forest Cover/Temperature interaction, while Great Horned Owls responded to Time of Evening, Wind Speed, and a Forest Cover/Wind interaction.

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CHAPTER 4

Thesis discussion and conclusions

DISCUSSION

Owls as indicators of ecological condition

Some owl species (e.g. Boreal or Barred Owls) may be excellent candidates as indicator species for ecological condition because they are easy to census (Hannon and McCallum 2003, O'Connell *et al.* 2000), and may be sensitive to habitat change (Landres *et al.* 1988). Similarly, they may have value as umbrella species, where their habitat areas encompasses that of many other species, because they have large home ranges and are non-migratory (Lambeck 1997, Noss 1999). Birds are also very popular with the general public and the mystique of the nocturnal owl may make them a flagship species for the conservation of natural habitat (Johnsgard 1988, Noss 1990). As well, the ability to use a species as an ecological indicator may depend on their presence or abundance being predictably associated with defined habitat characteristics (Dufrêne and Legendre 1997, Hutto 1998). However, I found that while all owl species were responsive to the amount of forest cover on the landscape, this relationship was generally weak, and only for the Great Horned Owl (not a high priority for conservation, given its generalist tendencies) was this relationship strongly supported. As well, owls exhibited a high level of variation in presence and abundance over time and space in relation to habitat change. These characteristics may suggest that owls are not ideal indicators of ecological integrity (Caro and O'Doherty 1999, Fleishman *et al.* 2000).

This lack of relationship may be due to small sample sizes or owl responses to habitat characteristics I did not measure, perhaps at smaller scales. I suspect that the owl

species studied here either did not have a strong relationship with habitat characteristics or were responding to habitat characteristics at a smaller scale or to landscape elements that I did not study (i.e. forest age classes, patchiness of forest types). My inability to collect habitat data on a small scale represents one limitation of this study. This problem is common in large-scale studies such as this, where effort and cost of collecting smaller-scale data across an entire region is prohibitive. As well, I, like other researchers, lacked reliable fine-scale GIS data in my study regions. These apparent weak relationships to habitat characteristics at the large-scale, and the prohibitive nature of collecting smaller-scale data across even a few owl territories, make this taxon a particularly poor indicator of habitat quality for logistical reasons.

For Great-horned Owls in particular, abundance can be a misleading measure of habitat quality. Populations of this species consist of both territorial pairs that are mated and may be attempting to breed, as well as a "floater" population of unmated males. While these "floaters" are not often detected in owl surveys, because they generally do not vocalize or respond to con-specific calls, they may be visually detected on survey routes etc. (Rohner *et al.* 2001). Perhaps more importantly, pairs holding a territory but not breeding, due to low prey abundance, are also less likely to respond to playbacks. Surveys would then underestimate owl populations, and may confound results, if prey density is variable across gradients of habitat fragmentation or availability.

Limitation of this study

Presence/abundance data and habitat condition

Other general issues with using presence or abundance as a measure of habitat condition is the lack of information on breeding success. While the need for large-scale regional information on the populations of taxa has been well documented (see Andren

1994), the sheer scale of such studies limits the type of data being collected, generally to presence or abundance. Information on breeding productivity is important in accurately determining the quality of habitat and predicting trends in population dynamics for long-term conservation purposes. If birds are being monitored and counted in sink landscapes (where the reproductive rate is not self sustaining, Pulliam 1988) they may be misleading, identifying poor habitats as high quality. For species such as owls and diurnal raptors, where nest monitoring is extremely labour intensive, presence or abundance data may be the only data available at a large scale.

Influence of prey abundance on owl response to changes in habitat

The abundance of prey is a critical aspect of predator population dynamics and plays a part in their habitat selection and may influence the way predators respond to changes in habitat availability and habitat configuration. While I did not collect information on prey populations during this study, the close relationship of Great-horned Owls to their prey populations may have significant impacts on the interpretation of the results of this study if changes in predator populations confound possible responses to habitat differences.

The productivity and diet composition of Great Horned Owls are closely tied to prey densities and availability (Rohner *et al.* 2001, Rohner and Krebs 1998). While Great-horned Owls demonstrate a numerical response to changes in snowshoe hare densities, (Rohner *et al.* 2001, McInvaille and Keith 1974) their territory size or density does not change (Rohner *et al.* 2001). This suggests that changes in prey densities over time and space within this study would not have had a significant impact on the detection of Great Horned Owls.

Work in the Kluane area (Rohner *et al.* 2001, Rohner and Krebs 1998) has shown that snowshoe hares comprise a large portion of Great Horned Owl diets, and the breeding success of this bird is closely tied to the 10-year cycles of hares. However, because of the rigid territoriality of these birds their abundance does not change dramatically with the fluctuation of hare abundance. Hence, owls may not fluctuate spatially with the density of their major prey item. Similar data for other owl species are sparse, though it is clear that Tengmalm's Owl abundance responds strongly to prey abundance over habitat characteristics (Hakkarianen *et al.* 1997).

Conclusions and future research directions

In this study all owl species examined were responsive to the amount of forest on the landscape, and only Barred Owls were likely to respond equally strongly to the configuration of forest as well. These results are consistent with other work of a similar nature on songbirds (Meyer *et al.* 1998, Trzcinski *et al.* 1999). However, the results from this study are relatively weak, only the Great Horned Owl can be confidently identified as responding strongly to the amount of forest cover over its configuration. Similarly, threshold responses across species are very weak, and only for the Great Horned Owl am I confident that a threshold exists at 60% forest cover. Barred Owls may exhibit a weak threshold somewhere between 45% and 60% forest cover, but Northern Saw-whet Owls appear to have no threshold response to the amount of forest cover. The most conclusive results from this study show that owl presence and abundance does differ among regions, however, I could not adequately test what regional characteristics owls were keying into.

The detection of owls is influenced by weather conditions and both the time of year and time of evening. In particular, Northern Saw-whet Owls are detected more often when temperatures are low, earlier in the breeding season (though Great Horned Owls

likely begin breeding earlier than Northern Saw-whet Owls). Great Horned Owls are detected more often when temperatures are higher; winds are light, and later into the evening. A positive interaction exists between the amount of forest and temperature for Northern Saw-whet Owls and between the amount of forest cover and wind for Great Horned Owls. It is critical to control for these factors as much as possible by limiting their variation when conducting owl-monitoring projects.

The results of this study call into question our ability to use road transects and call-surveys in monitoring populations of owls or drawing conclusions regarding habitat quality. It was clear from this study that short-term datasets, even over very large areas were not sufficient to confidently identify trends in owl populations, or large scale habitat associations. Significantly more work on the landscape and regional level habitat associations of owls in central Alberta is needed before we can begin to make appropriate land management decisions for these species. Work on the interaction between prey distributions and habitat configuration may also be warranted for these predator species that may be closely tied to their prey populations. Longer term monitoring of owls, especially species that may be more sensitive to habitat change, e.g. Boreal and Barred Owls, will provide the baseline data necessary to begin evaluating current owl management practices and develop appropriate conservation strategies for the future.

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APPENDIX 1

Owl responses to forest cover and configuration by region and year

METHODS

Methods for this appendix are identical to those in Chapter 2, except where noted below. Data analysis was conducted on each dataset by year and region individually (see Table 2-2. in Chapter 2).

Linear models

Species-specific configuration variables were determined *a priori* as the most likely to predict the presence or abundance of each species. For example, Great Horned Owls were most likely associated with edge density because they may use forest edges for hunting (Johnson 1993 and Rohner and Krebs 1996). Northern Saw-whet Owls may have been associated with a relatively high mean patch size and low patch size coefficient of variation, indicating a preference for landscape with few large patches of habitat for nesting and foraging opportunities both within forest interiors and at some forest edges (Hayward *et al.* 1993, Korpimaki 1988).

In all species the result of the step-wise regression analysis was variable across years and across regions. To maintain the comparability of the datasets I included all of the step-wise regression results in each analysis. This means that in each dataset all step-wise regression results from all datasets were included, resulting in up to a total of 13 models. No data are presented for the Barred Owl at Lac la Biche 2002 because in some cases models would not converge and no comparable set of models was available. This was likely due to the low number of detections in this dataset.

Breakpoint Models

Breakpoint models were fitted for each dataset following the methods described in Chapter 2.

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Table A-1. Best fit linear models for Great Horned Owls, by region and year. While forest edge density appears consistently as the best fit model in Ministik and Lac la Biche, none of these models conforms to the 3X rule for their dataset. The sign in brackets represents the sign of the coefficient for that parameter.

* = Model conforms to the 3X rule and we can be highly confident it is the best fit model of the set.

Dataset	Best-fit Model	AICc	*wi*	Deviance Explained (%)
LLB 2002	**(-) FED**	191.84	0.41	3.52
MSTK 2002	**(-) FED**	196.02	0.28	1.97
MSTK 2001	**(-) FED**	147.47	0.36	9.36
MNK 2002	**(+) Forest**	166.42	0.22	0.11
MNK 2000	**(-) FPSSD**	181.25	0.50	0.30

Table A-2. Best fit linear models for Northern Saw-whet Owls, by region and year. The amount of forest in the landscape and forest patch size standard deviation appear consistently as best fit models across regions and years. However, only one model meets the 3X rule. The sign in brackets represents the sign of the coefficient for that parameter.

* = Model conforms to the 3X rule and we can be highly confident it is the best fit model of the set.

Dataset	Best-fit Model	AICc	*wi*	Deviance Explained (%)
LLB 2002	**(+) FPSSD**	170.21	0.37	20.91
MSTK 2002	* **(+) Forest + (-) FMPS**	181.11	0.83	46.00
MSTK 2001	**(+) Forest**	151.32	0.36	14.89
MNK 2002	**(+) FPSSD**	149.62	0.29	1.71
MNK 2000	**(+) FPSSD**	152.47	0.33	3.55

Table A-3. Best fit linear models for Barred Owls, by region and year. Forest mean patch size appears most consistently as the best fit model for Barred Owls. Only in the Ministik landscape do these models meet the 3X criterion. Some models in the Lac la Biche dataset would not converge (likely due to low detections in this region), hence, no best fit model can be presented. The sign in brackets represents the sign of the coefficient for that parameter.

* = Model conforms to the 3X rule and we can be highly confident it is the best fit model of the set.

Dataset	Best-fit Model	AICc	*wi*	Deviance Explained (%)
LLB 2002	**No Model Convergence**			
MSTK 2002	* **(+) FMPS**	125.71	0.99	12.89
MSTK 2001	* **(+) FMPS + (+) FPSSD**	153.11	0.81	61.82
MNK 2002	**(-) FED**	133.84	0.50	0.45
MNK 2000	**(+) FMPS**	149.53	0.44	8.19

Table A-4. Best fit breakpoint models for Great Horned Owls, by region and year. No trend exists in these models over years or regions, though it is interesting to note that in 2002 the best fit breakpoint is progressively lower in regions where the amount of forest cover regionally is lower (see Table 2-1 for regional forest cover values). The sign in brackets represents the sign of the coefficient for that parameter. All models have a positive coefficient for forest cover.

* = Model conforms to the 3X rule and we can be highly confident it is the best fit model of the set.

Dataset	Threshold	AICc	*wi*	Deviance Explained (%)
MSTK 2002	**(-) 60**	197.32	0.17	3.84
MSTK 2001	**(-) 60**	151.29	0.17	7.92
MNK 2002	**(-) 45**	165.46	0.43	12.92
MNK 2000	**(+) 25**	184.99	0.27	13.50
LLB 2002	**(-) 30**	196.40	0.15	9.00

Table A-5. Best fit breakpoint models for Northern Saw-whet Owls, by region and year. A threshold response to the amount of forest cover may exist between 50% and 60% forest cover for Northern Saw-whet Owls, however, the evidence for this is weak from these results. The sign in brackets represents the sign of the coefficient for that parameter. All models have a positive coefficient for forest cover.

* = Model conforms to the 3X rule and we can be highly confident it is the best fit model of the set.

Dataset	Threshold	AICc	*wi*	Deviance Explained (%)
MSTK 2002	(-) **50**	183.77	0.19	42.74
MSTK 2001	(-) **60**	154.30	0.19	15.63
MNK 2002	(-) **60**	149.40	0.18	6.90
MNK 2000	(-) **35**	149.72	0.32	8.10
LLB 2002	(-) **60**	171.13	0.23	8.12

Table A-6. Best fit breakpoint models for Barred Owls, by region and year. Threshold responses to forest cover appear to be between 15% and 20% forest cover, there is strong evidence to suggest that these models (*) are the best fit of the set. The sign in brackets represents the sign of the coefficient for that parameter. All models have a positive coefficient for forest cover.

* = Model conforms to the 3X rule and we can be highly confident it is the best fit model of the set.

Dataset	Threshold	AICc	*wi*	Deviance Explained (%)
MSTK 2002	* **(+) 15**	253.82	0.79	37.25
MSTK 2001	* **(+) 10**	235.10	0.85	36.71
MNK 2002	* **(+) 25**	145.56	0.30	7.04
MNK 2000	**(+) 60**	151.27	0.23	8.72
LLB 2002	**(-) 10**	214.75	1.00	28.45

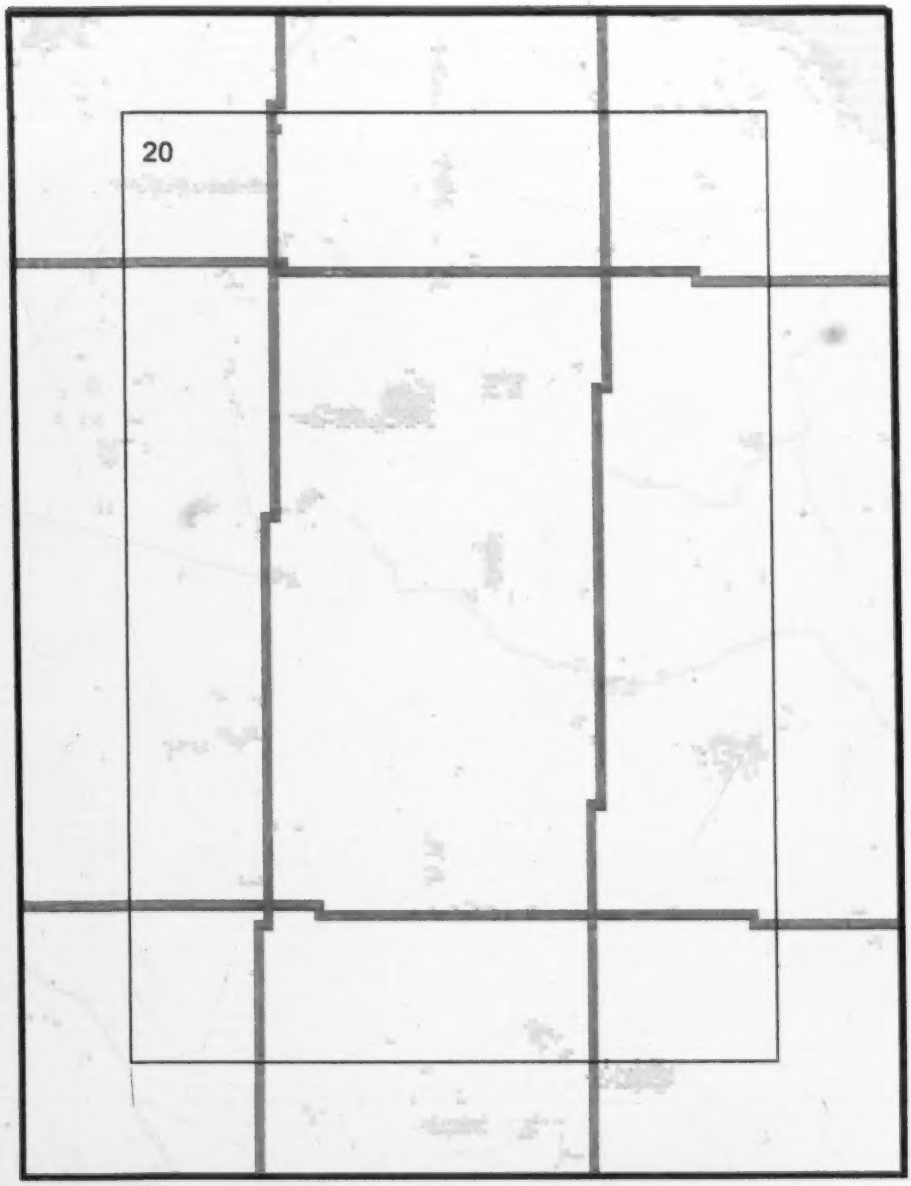

Figure A-1. Lac la Biche plot 20, an example of a landscape that is positively correlated with Axis 1. This landscape has high edge density, variable patch sizes, generally small patches, and low forest connectivity. Forest patches are in grey, roads are red, water is blue, and all non-forest habitat is white.

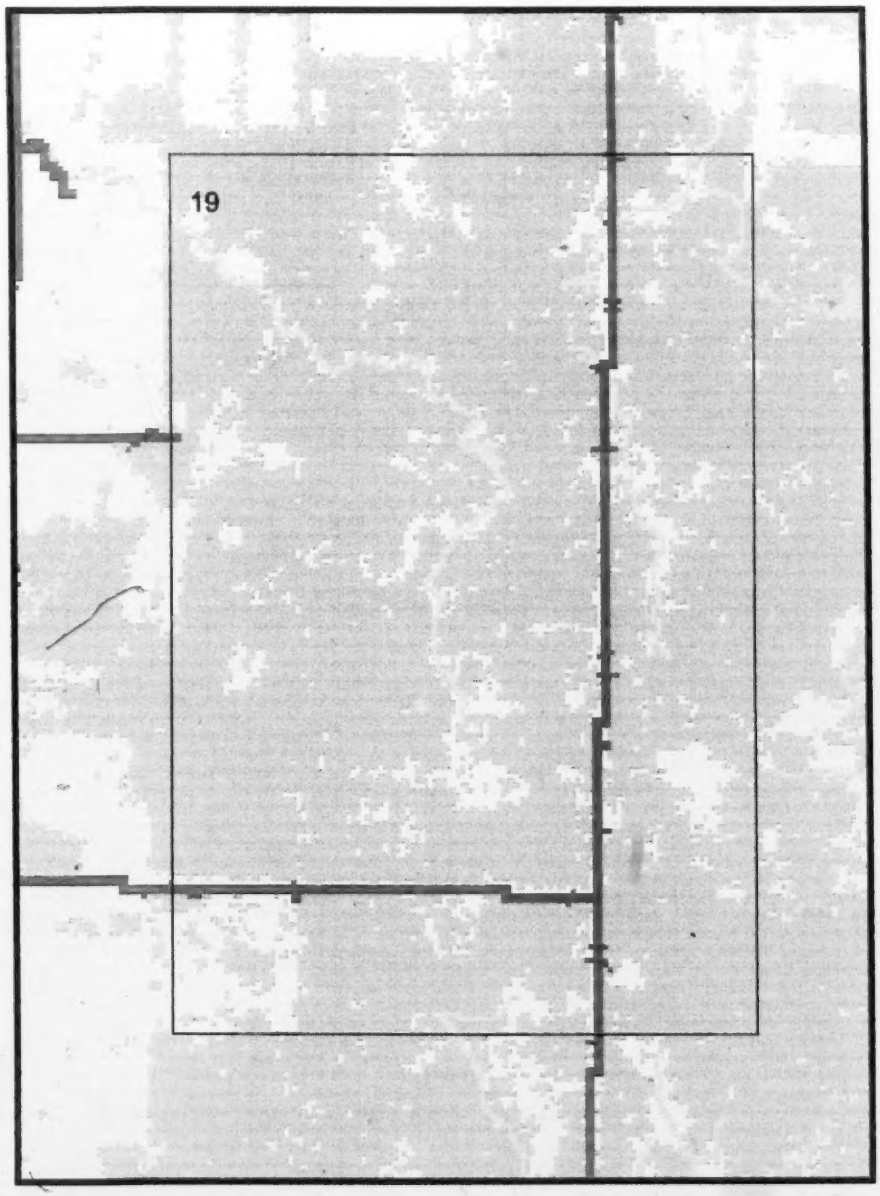

Figure A-2. Lac la Biche plot 19, an example of a landscape that is negatively correlated with Axis 1. This landscape has low edge density, homogenous patch sizes, large patches, and high forest connectivity. Forest patches are in grey, roads are red, water is blue, and all non-forest habitat is white.

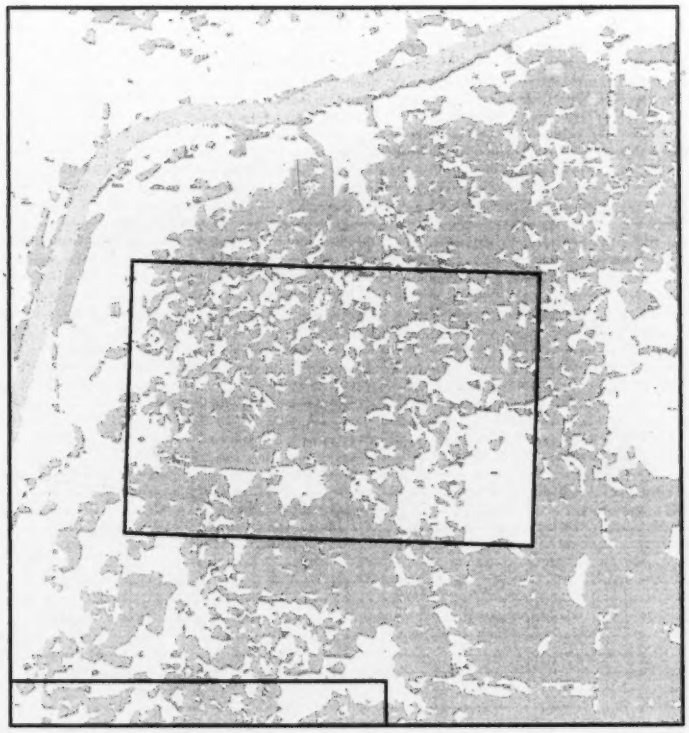

Figure A-3. Ministik plot 36; an example of a landscape that is positively correlated with Axis 2. This landscape has highly connected forest patches, high edge density, variable patch sized and relatively large patches. Forest patches are in grey, water is blue, and all non-forest is white.

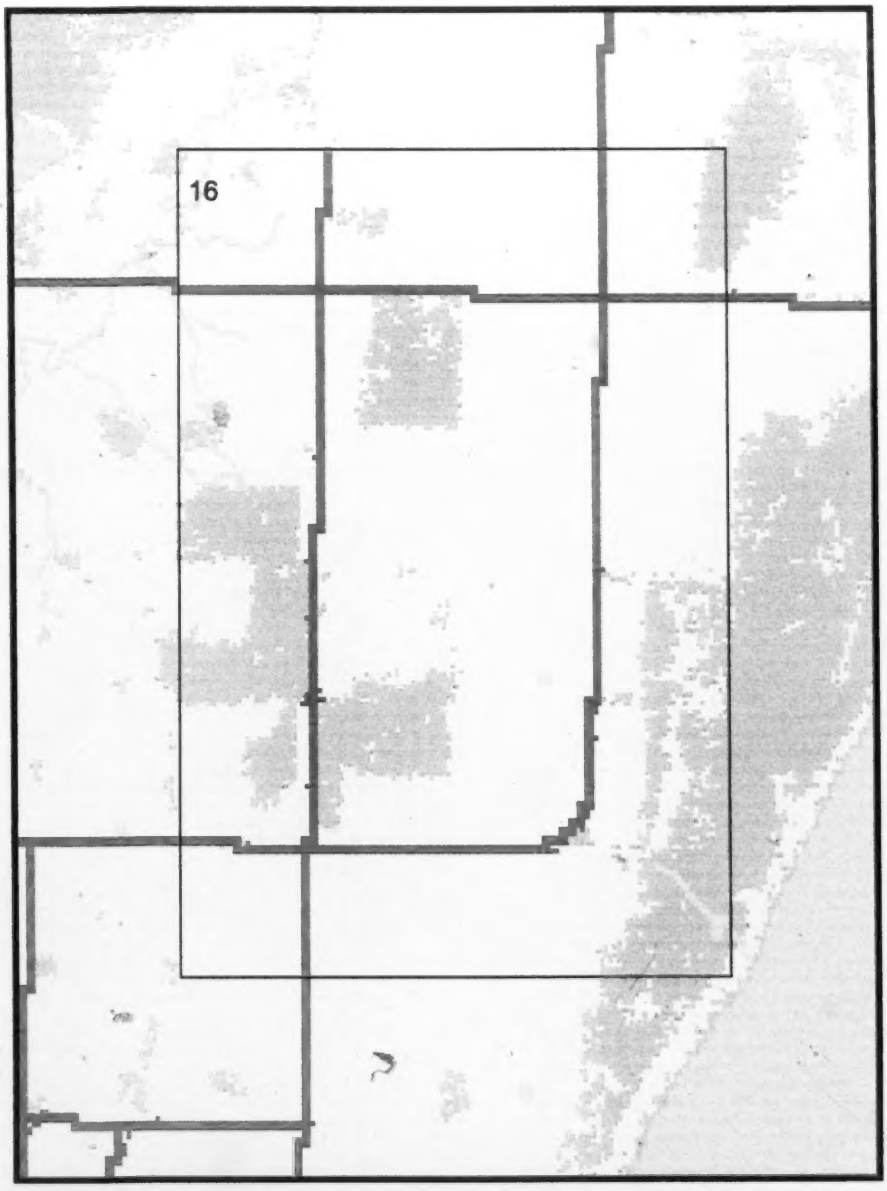

Figure A-4. Lac la Biche plot 16, an example of a landscape that is negatively correlated with Axis 2. This landscape has low forest connectivity, low edge density, homogenous patch sizes, and large patches. Forest patches are in grey, roads are red, water is blue, and all non-forest habitat is white.